AUSTRALIAN JOURNAL OF MARINE AND FRESHWATER RESEARCH

VOLUME 5

MELBOURNE
1954

AUSTRALIAN JOURNAL OF MARINE AND FRESHWATER RESEARCH

Published by the Commonwealth Scientific and Industrial Research Organization, in collaboration with the Australian National Research Council, and under the general direction of the Editorial Board (Dr. N. S. Noble (Chairman), Professor J. S. Anderson, Professor Sir Macfarlane Burnet, Professor L. H. Martin, and Professor J. G. Wood). A medium for the publication of the results of original investigations on sea, estuarine, and freshwater fisheries and cognate subjects

Issued as material becomes available, 7/6 per issue

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Australian Journal of Marine and Freshwater Research,
Commonwealth Scientific and Industrial Research Organization,
314 Albert Street, East Melbourne, C.2, Victoria

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MACROCYSTIS PYRIFERA (L.) AG. IN TASMANIAN WATERS

By A. B. Cribb*

(*Manuscript received October* 26, 1953)

Summary

An account is given of the taxonomy and distribution of *Macrocystis* in Australian waters, the development of the plant is outlined, and beds on the east coast of Tasmania are described.

Measurements of growth indicate that the most rapid elongation of the stipe takes place near the apex, and that a stipe may increase in length at a rate of at least 3.4 cm per day. The life of a stipe is estimated at between 7 and 10 months. Experiments show that the apical blade with a portion of the stipe may sometimes continue growth when severed from the holdfast. It is found that decrease in length of a blade caused by decay of tissue at the apex is for a time made good by meristematic activity near the base of the blade, but that finally meristematic activity ceases and decay eventually removes the whole blade.

Harvesting of *Macrocystis pyrifera* (L.) Ag. in selected areas over 2 yr gave no indication that beds are adversely affected by cutting the stipes 3 ft. below the surface at approximately 4-monthly intervals. The average yield obtained in three localities over 2 yr was 4 tons/ac, and on this basis the area surveyed could be expected to yield approximately 355,000 tons of wet weed or 35,000-44,000 tons of air-dried weed per year. Analyses of monthly samples of *Macrocystis* show an average alginic acid content of approximately 21 per cent. and an average mannitol content of approximately 8.7 per cent. on a dry-weight basis.

I. INTRODUCTION

In the past, *Macrocystis* has attracted considerable attention because of its high potash content, and interest in this aspect has resulted in detailed investigations of the plant in U.S.A. and New Zealand.

Today, interest centres on this familiar alga as a potential source of alginic acid rather than of potash, and the present investigation has been undertaken as a part of the seaweed programme of the Division of Fisheries, C.S.I.R.O., primarily to assess the resources of the species on the east coast of Tasmania.

II. TAXONOMY

After extensive experience of *Macrocystis* in the living state gained during the British Antarctic Expedition of 1839-43, Hooker (1847) united all the species of this genus then described under the name *M. pyrifera* Ag. These species had been segregated mainly on variations in bladder and blade, but Areschoug (1883), Skottsberg (1907), and Howe (1914) recognized the importance of the presence of a flattened rhizome in segregating some plants from *M. pyrifera.* Areschoug referred his plant to *M. angustifolius* Bory but Howe pointed out that Bory based most of his descriptions of this species on a plant from Australia. Howe found that this plant differs little from *M. pyrifera* except in its narrower blades, and stated that the earliest name for the small plant, i.e. the one with flattened rhizomes, from the west coast of South America is "*M. integrifolius*". Skottsberg (1907) referred a plant with flattened rhizomes to *M. pyrifera* forma *angustifolia.*

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* Department of Botany, University of Queensland, Brisbane, formerly of Division of Fisheries, C.S.I.R.O.

Setchell (1932) fully described the holdfasts of *Macrocystis,* mentioning much previous literature. He also recognized the two species, *M. pyrifera* (L.) Ag. and *M. integrifolia* Bory, the latter characterized by a strongly flattened prostrate rhizome which branches dichotomously or sub-dichotomously and is attached to the substrate by numerous branched haptera emitted along both lateral margins. In contrast to this prostrate type of attachment *M. pyrifera* develops a more or less conical holdfast formed by the mass of haptera given off from all sides of the lower part of the main stipe and its branches. These stipes are cylindrical or only slightly flattened and do not become prostrate.

Smith (1942, 1944) followed Setchell in recognizing these two species and used also the nature of the terminal blade as a basis for separation of the species, that of *M. integrifolia* being narrowly falcate, 5-15 times as long as broad, with rarely more than six young blades in process of differentiation, and of *M. pyrifera* being broadly falcate, 3-5 times as long as broad, and usually with 10-20 young blades in successive stages of differentiation. He gave the dimensions of the mature lateral blades as up to 40 cm long and 5 cm wide in *M. integrifolia* and up to 80 cm long and 40 cm broad in *M. pyrifera.*

Specimens have been examined from various points on the east coast of Tasmania between Bicheno in the north and Hythe in the south and there seems to be no doubt that they all belong to *M. pyrifera.* The holdfast (Plate 1, Fig. 2; Plate 2, Fig. 1) is always more or less conical or depressed conical and though sometimes there may be a slight flattening of the stipes just above and within the holdfast, the haptera are emitted on all sides and there is no development of the subligulate prostrate rhizome with haptera originating from the lateral margins.

Dimensions of mature blades are fairly variable but their width is nearly always considerably greater than 5 cm and their length at least 60 cm and usually more. Shape and dimensions of the terminal blade (Figs. 3-5) vary considerably from plant to plant and with age and other factors, but in general they do fall very clearly within the range of form and size given by Smith for *M. pyrifera.*

Macrocystis occurs in small quantities in a few places along the north coast of Tasmania and these plants seem to differ in some respects from the east coast specimens. The plants seen during the present survey are comparatively small, often not exceeding 12 ft in length, while those on the east coast may reach a length of at least 65 ft. The mature lateral blades are linear, generally no more than 3 cm broad and 60 cm long, while the terminal blade (Fig. 6) is of the narrowly falcate type figured by Smith (1942, 1944) for *M. integrifolia.* These characters suggest an affinity with *M. integrifolia,* but Hooker has already shown the futility of segregation based on characters of blade and pneumatocyst, and it is essentially on the nature of the holdfast that the determination must be made. These smaller north coast plants possess correspondingly smaller holdfasts than east coast plants but though often somewhat irregular or distorted they are definitely of the conical type in which haptera are emitted from all sides of the main axis and its lower branches, and in the specimens seen there is no sign of the prostrate subligulate rhizome. These plants cannot be referred to the typical *M. integrifolia* of the west coast of America as figured by Howe (1914), Setchell and Gardner (1925), Setchell (1932), and Smith (1942, 1944), but the Australian plant which Collins claimed was used by Bory for his description of *M. angustifolia* (*M. augustiformis*) may be of this form. However, in view of the opinions expressed by Hooker, it would be unwise to pronounce these smaller specimens as taxonomically distinct from *M. pyrifera* before a large range of specimens has been examined from the Australian coast, particularly from localities where the two forms geographically approach one another.

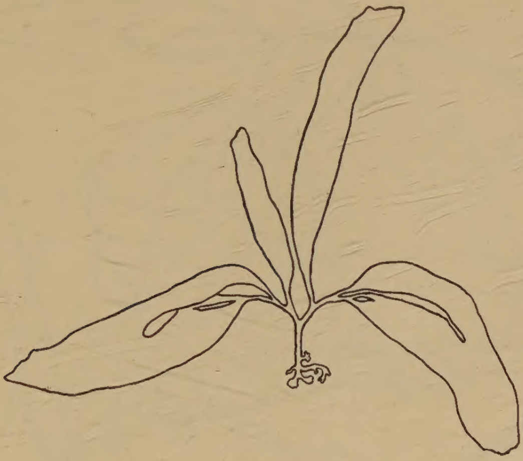

Fig. 1.—Young sporophyte of *Macrocystis pyrifera.*

Macrocystis occurs on the coast of Victoria and south-eastern South Australia, and the herbarium material available, though inadequate and wanting holdfast tissue, shows a resemblance to the form from the Tasmanian north coast rather than to the one from the east coast. Under *M. pyrifera* var. *dubenii* Aresch., Harvey (1862) figured a plant from outside Port Phillip, apparently of the narrow-blade type.

III. THE MACROCYSTIS PLANT AND ITS DEVELOPMENT

The development of *Macrocystis* is discussed by several authors, including Skottsberg (1907), Brandt (1923), and Setchell (1932). The young sporophyte consists of a simple stipitate blade resembling a juvenile *Ecklonia* or *Laminaria*. This primary blade splits equally and before the division is complete each secondary blade thus formed splits unequally. The outer product of each secondary split develops a thickened margin at the base on the outer side and as this blade splits repeatedly in an asymmetric manner the thickened margin gives rise to the stipe, which elongates and so separates the newly formed blades (Figs. 1, 2). These at first are carried unilaterally but by a subsequent rearrangement become sub-distichous. A pneumatocyst or bladder, generally somewhat pyriform, early develops at the base of each of these lateral blades so that the whole stipe is buoyed up and the upper parts float along the surface, often for a distance of several yards (Fig. 7).

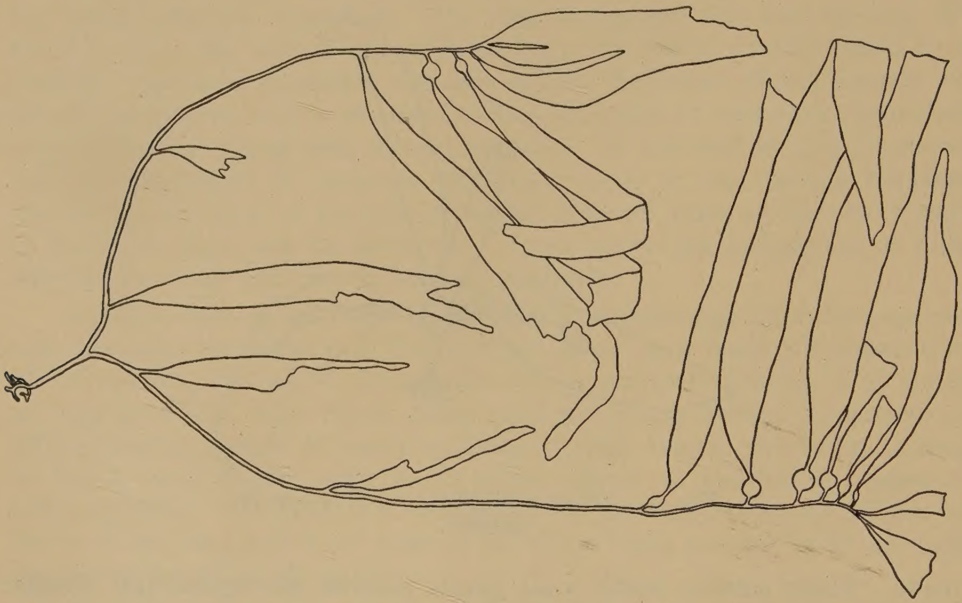

Fig. 2.—Young sporophyte of *Macrocystis pyrifera* with two rapidly elongating stipes.

The inner product of each secondary split does not develop a bladder and though for a time remaining arrested, it eventually undergoes asymmetric splitting, one product giving rise to an elongate stipe and the other again remaining arrested for a time until it in turn is asymmetrically split. Generally, the first few blades cut off by a rapidly splitting terminal blade fail to develop bladders, and most of these at a later date are capable of undergoing asymmetric splitting to give rise to a stipe and arrested blade. Sometimes an arrested blade may undergo repeated symmetrical splitting so that a *Lessonia*-like tuft of arrested blades is formed. Thus in an old plant there may be, just above the holdfast, a very large number of arrested blades, each a potential source of a new stipe and another arrested blade.

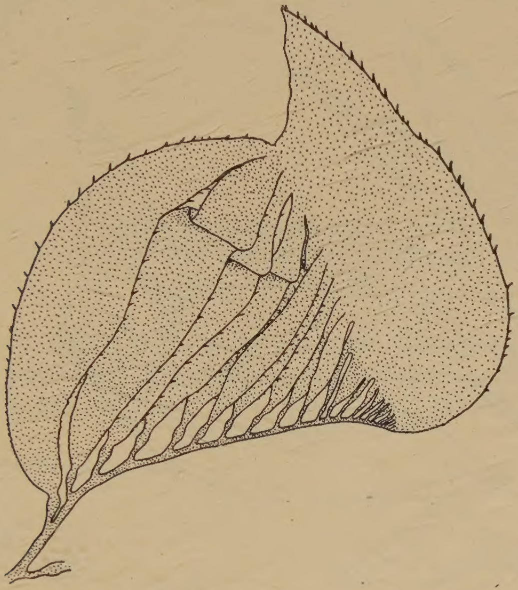

Fig. 3.—Terminal blade and apical portion of stipe of *Macrocystis pyrifera* from the east coast of Tasmania.

A blade which has developed a bladder does not normally split, but on very rare occasions such blades have been found with a median split developed to a certain extent. Usually the rapidly elongating stipe remains quite unbranched except near the base, but on three occasions plants bearing forked stipes have been found and this branching appears to have arisen through a newly formed lateral blade's assumption of the function of a terminal blade. Other abnormalities such as incompletely separated or distorted blades and bladders sometimes occur but are rare.

When a stipe is nearing the end of its actively growing period certain changes take place in the terminal blade. There is a reduction in the rate of splitting and in the number of new blades in process of formation. The thickened margin increases in thickness and finally the terminal blade ceases to divide and forms a bladder at its base. When this happens growth in length practically ceases and after maturation of the parts already laid down, the blades and bladders gradually decay and the stipe finally breaks away, the break generally occurring close to the holdfast.

The blades are lanceolate in shape and in robust specimens from exposed positions may attain a length of 2 m and a diameter of 15 cm or more. The width in proportion to length varies somewhat from plant to plant and occasional specimens may be ovate-lanceolate while other extremes may be almost strap-shaped.

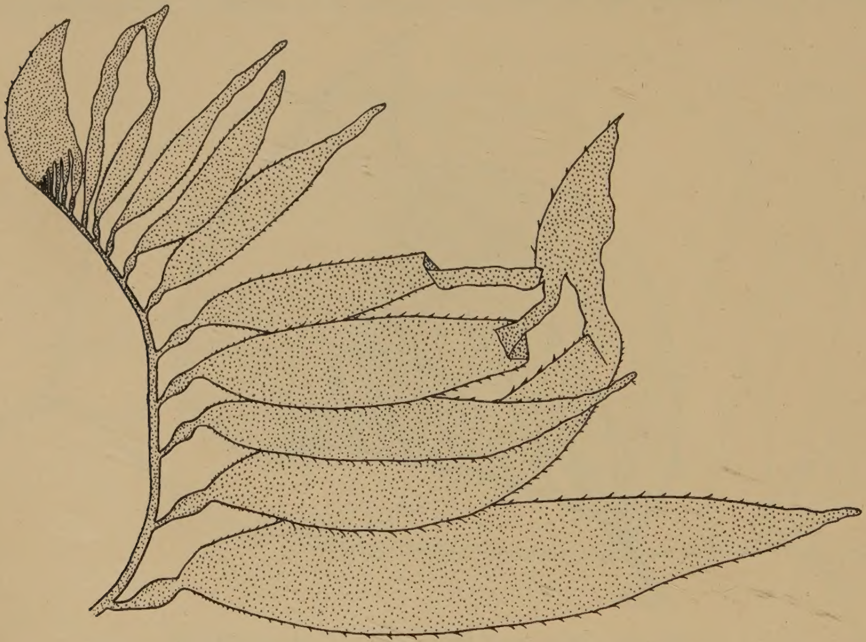

Fig. 4.—Terminal blade and apical portion of stipe of *Macrocystis pyrifera* from the east coast of Tasmania.

The gas-filled pneumatocysts are typically pyriform and constricted below into a short stipe, but they vary in size and shape with the position on the stipe and habitat, and extreme forms may be spherical or clavate. Mature pneumatocysts on vigorous plants from exposed localities are often pyriform-clavate and attain 8 cm in length and at least 2 cm in width, while in sheltered positions the dimensions are usually smaller and the shape tends to be pyriform or pyriform-globose. The various forms have been figured by Skottsberg (1907) and Brandt (1923).

When young, the pneumatocysts are lined with a close dry tomentum but with increasing age droplets of water appear on this surface which finally becomes quite wet, and old senescent bladders sometimes accumulate a considerable amount of water, which is probably responsible for often keeping old decaying stipes lying along the sea bottom.

The diameter of the stipe varies generally between 6 and 10 mm, being narrower in the lower than in the mid parts. Throughout most of its length it is cylindrical or almost cylindrical but at the base where branching has taken place there may be some flattening. In Australia the lengths of the plants do not seem to have been exaggerated. Harvey (1862) gave the length of Australian specimens as 50-100 ft or more, while Lucas (1936) set the figure at 9-30 m. The longest plant measured during the present survey was one from Port Arthur which reached 65 ft from holdfast to terminal blade (Plate 1, Fig. 1), but greater lengths

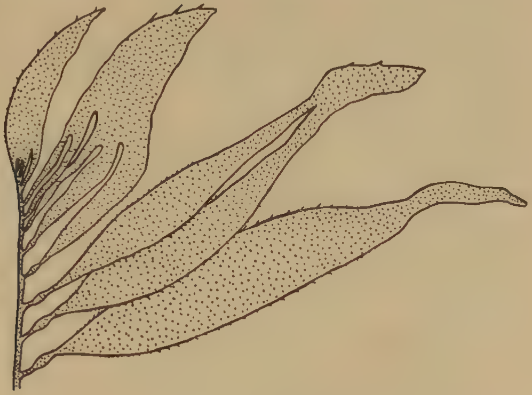

Fig. 5.—Terminal blade and apical portion of stipe of *Macrocystis pyrifera* from the east coast of Tasmania.

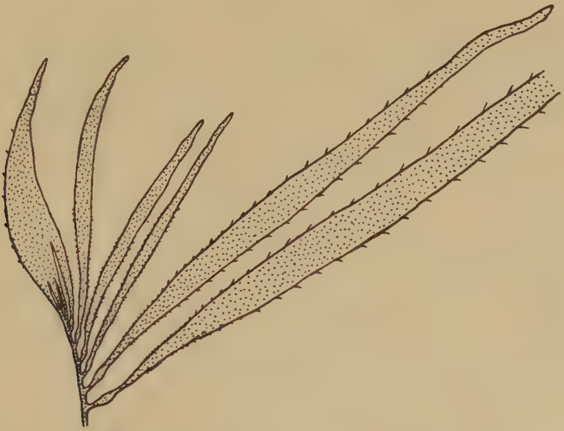

Fig. 6.—Terminal blade and apical portion of stipe of the smaller form of *Macrocystis* from the north coast of Tasmania.

almost certainly occur in the more exposed beds in deeper water. Hooker (1847) gave an estimated maximum length of 700 ft for plants in the Crozet Is., while according to Harvey (1858) "Bory St. Vincent attributes to them a length of 1500 ft." These reports are, however, only estimates and the lengths may be exaggerated. Frye, Rigg, and Crandall (1915) measured plants on the Californian coast and found a maximum length of 45.7 m, and the greatest measured length recorded appears to be that of 195 ft given by Cotton (1915) for a plant in the Falkland Is.

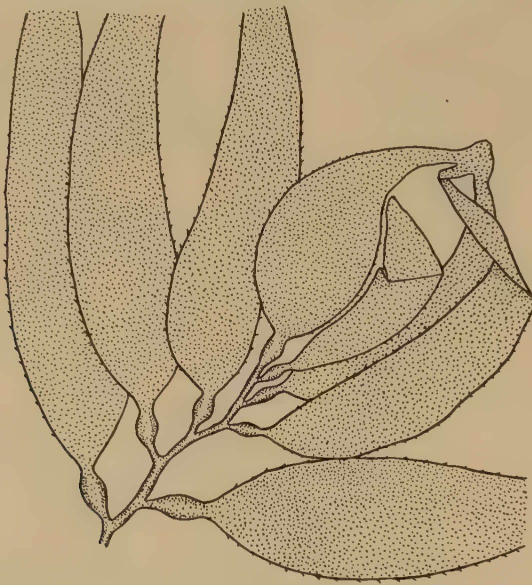

Fig. 7.—Apical portion of a stipe of *Macrocystis pyrifera* on which a bladder has formed at the base of the terminal blade.

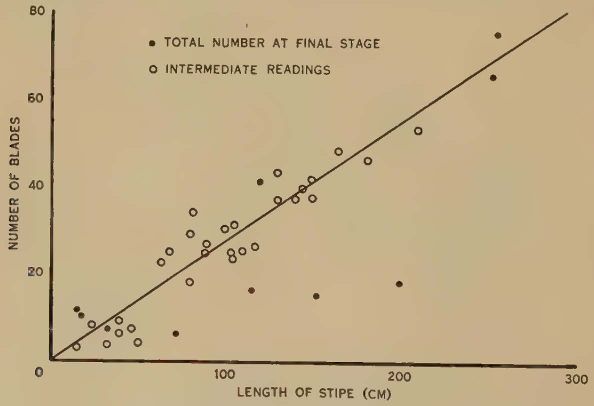

Fig. 8.—Relationship between number of blades and length of stipe.

The dichotomously branched haptera, generally 2-5 mm in diameter, arise progressively higher up on the main stipe and its branches, finally forming an intricate compact and somewhat conical mass of interlaced haptera in which the bases of the main stipe and its lower branches are embedded. Where a hapteron meets the substrate it expands into an irregular attachment disc, but as new haptera grow down over the mass already formed the older ones decay and in an old holdfast it is only the outer few layers of haptera which are alive and effective in anchoring the mass. Brandt (1923) noted that the larger the holdfast becomes the longer the haptera have to be to reach the substrate, and he stated, "the increasing difficulty of producing hapteres of sufficient length to secure it to its anchorage is one of the factors determining the length of life attained by the plant".

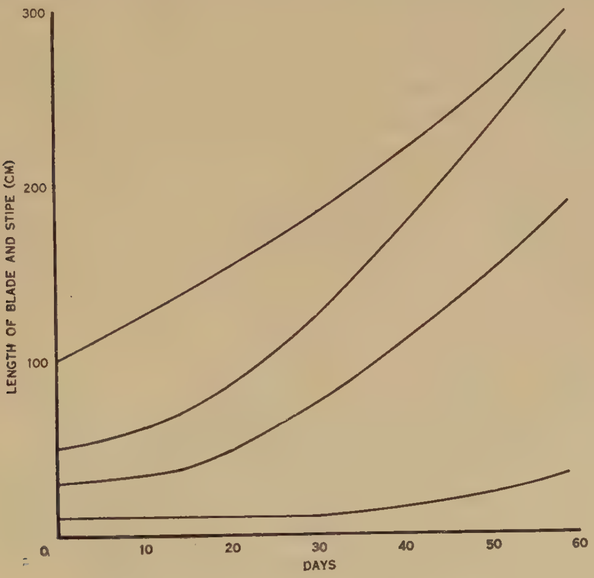

Fig. 9.—Average growth increment.

The largest holdfast measured during the survey was one cast up at Eaglehawk Neck and this reached 60 cm in basal diameter. These holdfasts are very securely anchored to the sea floor and it is not unusual for fishermen to moor boats up to 30 ft long to a bundle of *Macrocystis* stipes.

The anatomy of *Macrocystis* has been discussed by Skottsberg (1907) and Sykes (1908).

In Tasmania, the holdfast does not appear to provide a suitable substrate for algal colonization. *Caulerpa hypnoides, Phacelocarpus labillardierii,* and other species have at times been found with their basal parts immersed among the mass of haptera but more usually the holdfast is bare of algal epiphytes. Not even the encrusting lithothamnia often found on *Ecklonia* holdfasts seem able to exist here. However, the holdfasts, particularly the decaying portions, do shelter an enormous number and variety of animals, including small fish and eels, crabs, isopods, amphipods, worms, hydroids, bryozoans, molluscs, and sponges. The richness of this fauna was also noted by Andrews (1925, 1945), Fosberg (1929), and Hartwig (1860).

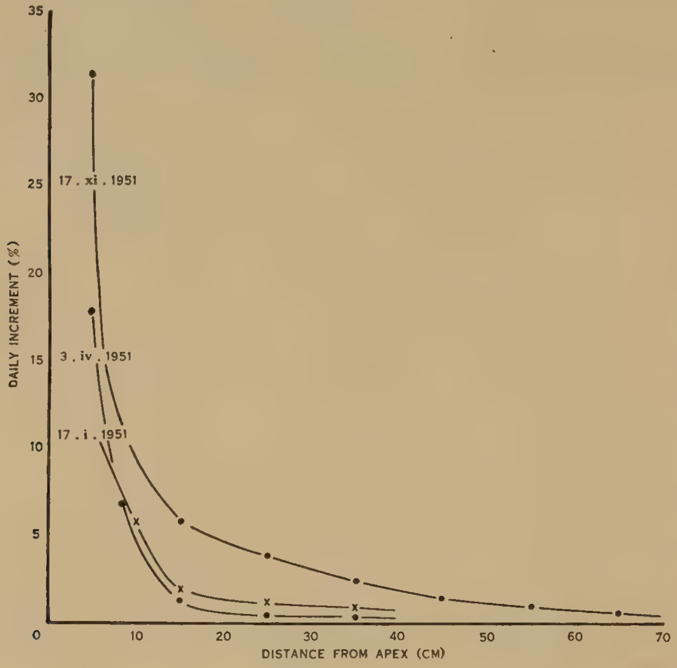

Fig. 10.—Decrease in daily increment.

A number of animal epiphytes occur also on blades, pneumatocysts, and stipes. One of the most common is *Membranipora,* which forms extensive white, circular or irregular, closely adherent patches over the surface. Where the colonies develop on immature blades some puckering of the surface often results. The small spiral tubes of *Spirorbis* are sometimes present in large numbers and a hydroid may occur fairly densely on some blades. A small pink gastropod, *Cantharidus* (?) sp., is found in small numbers on the blades but does no apparent harm to the kelp.

On healthy plants algal epiphytes are usually fairly rare, though sometimes, particularly in the more sheltered positions, *Polysiphonia fuscescens* may occur fairly densely, and *Myrionema densum* may form numerous small, rounded, brown spots often not more than 2-3 mm in diameter. Badly decayed blades sometimes carry a fur of *Ectocarpus confervoides* and on occasions *Polysiphonia* spp., and *Ceramium* spp. have also been found on these blades. Harvey (1863) described *Porphyra woolhousiae* growing on the marginal teeth of the blades of *Macrocystis* in Tasmania, but this species has not been found during the present investigation.

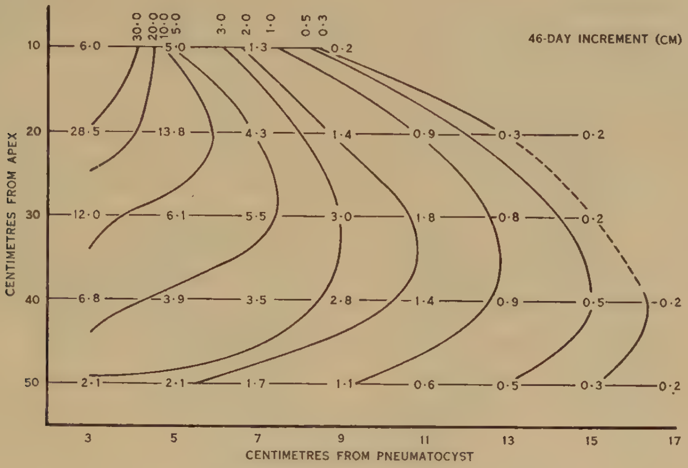

Fig. 11.—Total increment of blades in 46 days.

IV. REPRODUCTION

Unilocular sporangia mixed with paraphyses form extensive irregular sori on both surfaces on arrested bladderless blades, sometimes almost the whole surface being covered with the sorus, which gives the blade a darker and thicker appearance. Sori sometimes occur on the floating blades at the surface of the water but here they are generally, though not always, restricted to the corrugations in the basal part of the blade. In a senescent blade it is often the fertile areas which are the first to decay. Sori have been found on the submerged blades during all months of the year but occur commonly on the surface blades only during the colder months. Hoffman (1911) reviewed the literature concerning the fructification of *Macrocystis*.

Brandt (1923), Delf and Levyns (1926), and Levyns (1933) discussed the development of the filamentous gametophyte and young sporophyte, and more recently Papenfuss (1942), working on South African plants, gave a complete account of this development.

Glass and bakelite plates were suspended from a permanently moored boat at a depth of approximately 6 ft in close proximity to a *Macrocystis* bed at Port Arthur. It was hoped that examination of these plates at intervals might yield some information as to the periods of development of the *Macrocystis* sporelings. However, monthly examinations over a period of 12 months failed to reveal anything which could be recognized as a gametophyte or young sporophyte.

Walker (1952) investigated *Macrocystis integrifolia* and found gametophytes with the haploid complement of 16 chromosomes and sporophytes with a diploid number of 32.

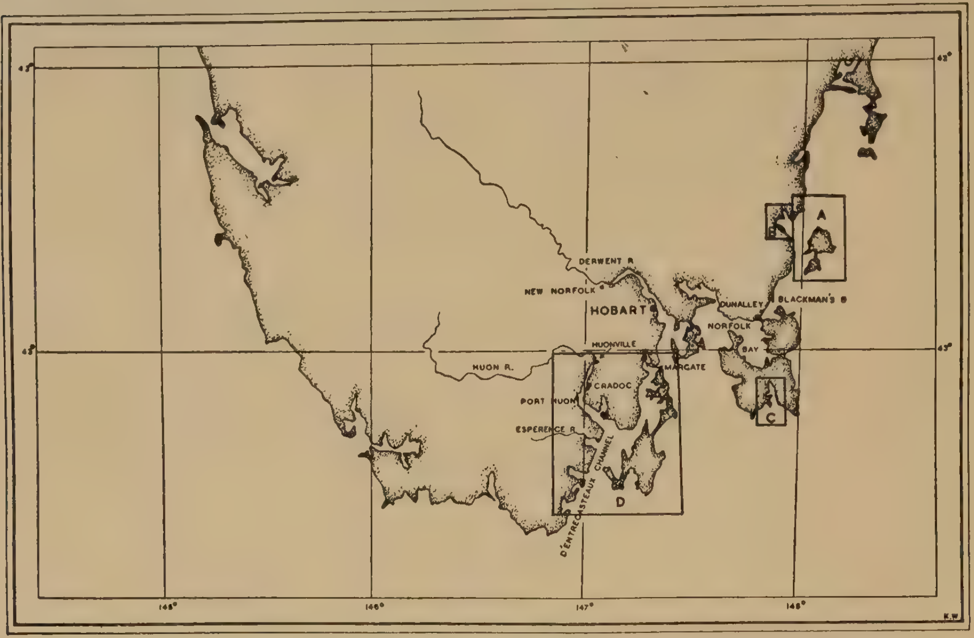
42°
42°
DERWENT R.
NEW NORFOLK
HOBART
DUNALLEY
BLACKMAN'S B.
NORFOLK
BAY
HUONVILLE
HUON R.
MARGATE
CRADOC
PORT HUON
ESPERENCE R.
D'ENTRECASTEAUX CHANNEL
A
C
D
43°
43°
145°
146°
147°
148°
K.W.

Fig. 12.—Key to the location of areas surveyed in southern Tasmania.

V. Distribution

As Skottsberg (1907), Setchell (1932), and Fritsch (1945) have shown, the main distribution of *Macrocystis* is circumpolar in the southern hemisphere between latitudes 40° and 60°S. In New Zealand, Rapson, Moore, and Elliott (1943) reported it south of approximately 40°S., mainly on the east coast. It occurs on the west coast of South Africa, according to Papenfuss (1942) between 33° 24′S. and 34° 8′S., and on the west coast of South America extends almost to the equator, reappearing in North America in the neighbourhood of the Tropic of Cancer and reaching Sitka in the north. Setchell (1932) and Smith (1942) pointed out that part of the range on the west coast of America is occupied by *M. integrifolia*.

In Australia, *Macrocystis* is known to occur sparsely on the extreme south-east coast of South Australia, and extends round the coast of Victoria and for a short distance along the coast of southern New South Wales. In Tasmania, small patches of *Macrocystis* occur on the north coast in a few places such as Low Head, Port Sorell, and Stanley but there seem to be no beds of commercial importance along this coast. Large beds have been reported from Port Davey on the south-west coast but apart from this report nothing is known of the distribution along the relatively inaccessible west coast. Numerous beds of varying size occur along the whole of the east coast from Eddystone Point in the north to Recherche Bay in the south, the largest of these being in the vicinity of Spring Bay and Actaeon I.

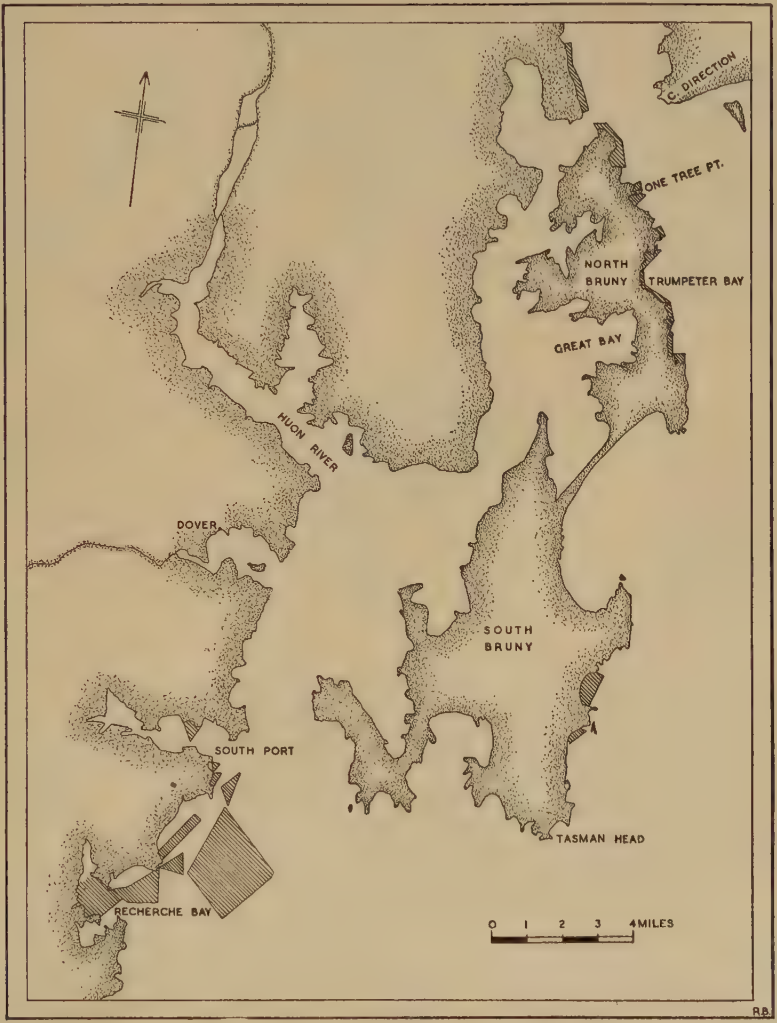
C. DIRECTION
ONE TREE PT.
NORTH BRUNY
TRUMPETER BAY
GREAT BAY
HUON RIVER
DOVER
SOUTH BRUNY
SOUTH PORT
TASMAN HEAD
RECHERCHE BAY
0 1 2 3 4 MILES
R.B.

Fig. 13.—Location and extent of *Macrocystis* beds surveyed, area *D.*

Setchell (1932) has shown that *Macrocystis* is distributed in waters with a surface temperature varying from 0 to 20°C. An examination of the Oceanographical Station List (1951) reveals that on the south-east coast of Australia too, *Macrocystis* is in the main confined to waters where the surface temperature does not exceed 20°C, and it is only in the northern extremity of the range that the water temperature may very rarely exceed this figure.

The available surface water temperatures for Porth Arthur, where much of the experimental work was carried out, are given in Table 1. These figures are the averages of weekly readings made at 10 a.m., 12 noon, and 3 p.m.

VI. THE MACROCYSTIS BEDS

Large beds in the vicinity of Spring Bay and Actaeon I. are up to ½ mile in diameter but in many places the *Macrocystis* occurs along the shore in a narrow fringing bed of variable width sometimes in sheltered localities as narrow as 10-20 ft, but generally considerably wider (Plate 2, Fig. 2). On calm days the margins of the blades often project in graceful golden arcs above the surface of the water which in dense beds is completely covered by the mass of floating stipes, bladders, and blades. Blue cranes often rest on the bed and small boats find it almost impossible to penetrate.

TABLE 1

AVERAGE MONTHLY SEA TEMPERATURES AT PORT ARTHUR

	Temperature (°C)		Temperature (°C)
October 1950	13.8	October 1951	14.0
November 1950	14.7	November 1951	14.5
December 1950	15.6	December 1951	14.5
January 1951	17.3	January 1952	16.3
February 1951	17.3	February 1952	17.8
March 1951	16.9		

The beds give the water a somewhat oily appearance and by "damping down" the swell do to a limited extent reduce the surf action on the shore. This is in contrast to the position in South Africa where Isaacs (1937) described *Macrocystis* as occurring "where it is protected from the full force of the open sea by a palisade of *Ecklonia*".

In Tasmania, the *Macrocystis* bed is frequently separated from the shore, at least in sheltered positions, by a dense band of *Phyllospora comosa* which, within its area, excludes almost completely most other macroscopic algae with the exception of the encrusting lithothamnia. The *Phyllospora* appears at about extreme low-water mark of spring tides and extends downwards for 4-6 ft in sheltered positions, and to greater depths in more exposed localities. Where *Phyllospora* is absent or sparse in sheltered positions small plants of *Macrocystis* are occasionally found at and just below the position of extreme low-water mark of spring tides, but the stipes, bladders, and blades of these plants are constantly coming into contact with the rocky shore so that they generally have a battered appearance. As the delicate terminal blade of each stipe is early destroyed, growth in that stipe practically ceases and plants never reach maturity and seldom exceed 2-3 ft in length. In exposed positions even small plants would be quite unable to withstand the battering received in the upper sublittoral, and here the beds always occur in deeper water out of reach of the shore.

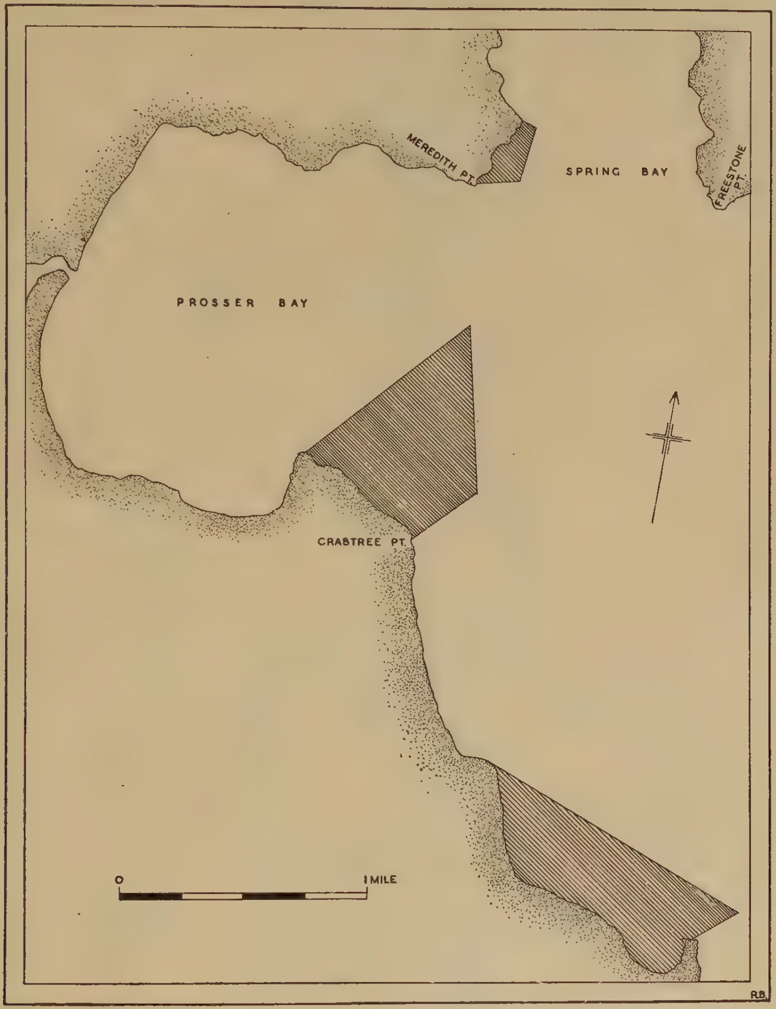

Fig. 14.—Location and extent of *Macrocystis* beds surveyed, area *B*.

The *Macrocystis* holdfasts require a rocky substrate for attachment and the outer limits of fringing beds are often determined by the appearance of a sandy bottom rather than by increasing depth. Fishermen report that after destruction by storms beds may occasionally fail to reappear for a number of years. Since Rapson, Moore, and Elliott (1943) have shown that at Thorndon in New Zealand a plant may grow from spore to maturity within 12 months, it seems possible that this failure to regenerate may be caused by the deposition over the original rocky bottom of a layer of sand which in time is removed, thus allowing the re-establishment of the bed. This deposition of sand over a rocky bottom occurred in the plot used for trial harvests at Hythe (Southport) and resulted in the disappearance of *Macrocystis*.

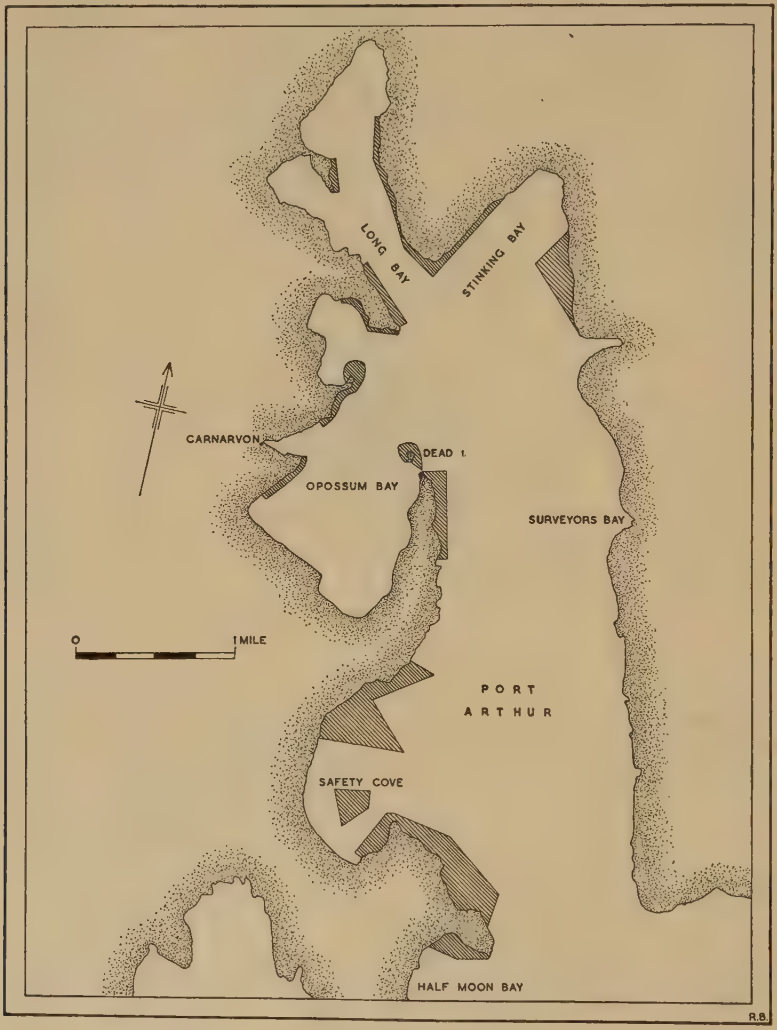
LONG BAY
STINKING BAY
CARNARVON
DEAD I.
OPOSSUM BAY
SURVEYORS BAY
0
1 MILE
PORT ARTHUR
SAFETY COVE
HALF MOON BAY
R.B.

Fig. 15.—Location and extent of *Macrocystis* beds surveyed, area *C*.

Hooker (1847) stated that "one thing alone it requires, and that is, a mean depth of six or more fathoms". However, as already mentioned, occasionally juvenile plants may be found in Tasmania in sheltered localities at about the level of extreme low-water mark of spring tides, and plants frequently appear immediately outside the band of *Phyllospora comosa* at a depth of 4-6 ft. But certainly, plants in these localities, though apparently healthy, are small in all their parts and best development is shown in deeper water.

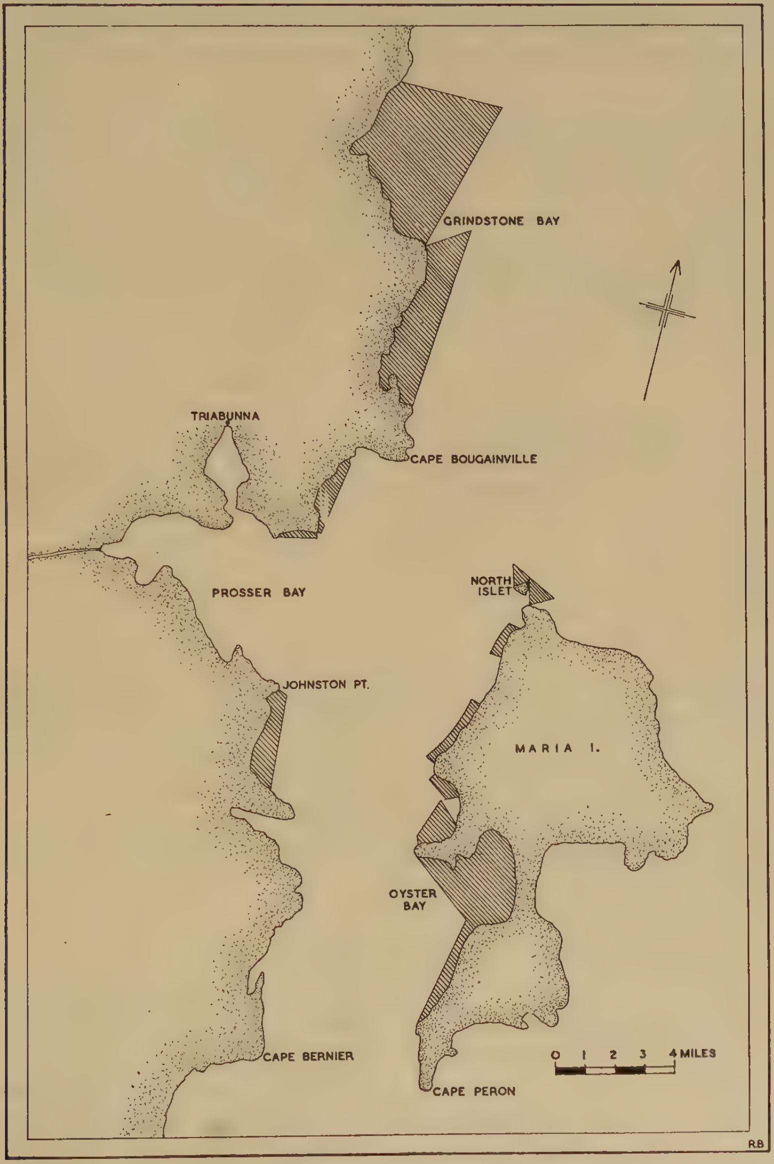
GRINDSTONE BAY
TRIABUNNA
CAPE BOUGAINVILLE
PROSSER BAY
NORTH ISLET
JOHNSTON PT.
MARIA I.
OYSTER BAY
CAPE BERNIER
CAPE PERON
0 1 2 3 4 MILES
RB

Fig. 16.—Location and extent of *Macrocystis* beds surveyed, area *A*.

Frye, Rigg, and Crandall (1915) found *Macrocystis* on the Californian coast growing at depths of 2½-14 fm and Cotton (1915) quoted a letter in which it is stated that *Macrocystis* grows at a depth of at least 16 fm in the Falkland Is.

At Port Arthur, soundings made in *Macrocystis* beds have shown depths up to 45 ft. No soundings were made in the larger exposed beds near Spring Bay and Actaeon I. but according to Admiralty charts of these areas the main beds exist in water of 4-8 fm and some probably reach a depth of 10-13 fm.

The plants are able to stand great variation in degree of exposure, some beds, including those at Grindstone Bay and Actaeon I., being subject to maximum exposure while at Port Arthur, narrow fringing beds thrive in the most sheltered bays, and occasional plants have been found even on rocky outcrops in a *Zostera* association which occupies extensive sand-mud flats in the most sheltered localities. In New Zealand, Moore (1943) described a branched unattached form which lies submerged close to a mud-sand bottom in quiet bays, but no such form has been found in Tasmania.

TABLE 2

RESULTS OF TAGGING STIPE 5 AND 10 CM FROM APEX, 7.vi.1951

Original Tagged Interval (cm)	Length of Tagged Interval After 14 Days (cm)						
	Stipe 1	Stipe 2	Stipe 3	Stipe 4	Stipe 5	Stipe 6	Stipe 7
Apex-5	16	17	14	16	21	19	14
5-10	11	12	10	10	13	11	12

Where *Macrocystis* forms very dense stands it may reduce the light intensity to such an extent that few algae except the shade-tolerant encrusting lithothamnia are able to exist beneath the canopy. But in many places, at least to depths of 20 ft, there is an understorey of variable density generally dominated by *Ecklonia radiata* but often with a variety of other algae, particularly phaeophytes such as *Zonaria subarticulata*, *Halopteris* sp., and *Cystophora* spp.

VII. MEASUREMENT OF GROWTH

Growth of the stipe was investigated by attaching tags at various points and measuring the increased distance between adjacent tags after a given interval of time. The tags used were grey or white plastic discs 1.5 cm in diameter, each carrying a distinguishing number and pierced through the centre by a small hole. At first, these were attached by a silver wire piercing the stipe but it was found that this frequently caused immediate or subsequent snapping of the stipe at the point of injury. Tags were then attached by twisting the wire loosely round the stipe and though this allowed free movement between adjacent bladders the inaccuracy introduced in this way was in most cases not serious. This method suffered from the disadvantage that in the tags placed near the terminal blade the wire gradually cut into the stipe as the latter increased in size and this sometimes resulted in fracture of the stipe at the point of attachment. Movement of tag and wire also resulted occasionally in severe chafing of the stipe, so attachment by means of rubber bands was tried and proved to be satisfactory. The bands had little or no cutting or chafing effect and were found to be in good condition after immersion for 4 months.

Throughout the investigation of the growth it has been found convenient to regard the position of the youngest split in the terminal blade as the apex of the stipe.

TABLE 3

RESULTS OF TAGGING STIPE 5, 10, 15, 20, AND 25 CM FROM APEX, 22.x.1951

Original Tagged Interval (cm)	Length of Tagged Interval After 7 Days (cm)			
	Stipe 1	Stipe 2	Stipe 3	Stipe 4
Apex- 5	7	7	8	7
5-10	6	7	6	7
10-15	5.5	6	5	6
15-20	5	5	5	5
20-25	5	5	5	5

Tagging was carried out generally not more than approximately 100 ft from the shore in positions which could be fairly accurately fixed by taking lines with features on land, and though each tagged stipe was additionally marked by a 1-in. bark cork attached at some point by fishing twine, considerable difficulty was often experienced in relocating the plants. Marking with anything more conspicuous than small corks was not considered advisable as a small minority of fishermen unsympathetic towards the investigation might have found and removed markers such as large painted corks. It was found once that children had removed tags, and some plants were probably lost when fishermen cut away kelp while recovering cray pots set along the fringing beds. Loss in this way, together with depletion caused by storms, considerably reduced the number of plants recovered, and sometimes all or most of a group were lost.

TABLE 4

RESULTS OF TAGGING STIPE 10 AND 30 CM FROM APEX, 16.x.1951

Original Tagged Interval (cm)	Length of Tagged Interval After 7 Days (cm)				
	Stipe 1	Stipe 2	Stipe 3	Stipe 4	Stipe 5
Apex-10	16	15	15	16	16
10-30	23	25	25	28	21

(*a*) *Growth of Stipe*

Macrocystis stipes were tagged in the manner described at various points within Port Arthur and representative results of the measurements made are shown in Tables 2-6.

These results indicate that the greatest rate of increase in length takes place within the apical 30 cm of the stipe and that behind this region there is a rapid falling off in the rate of elongation, so that at some point between 30 and 60 cm from the apex growth in length becomes extremely slow. The exact position of the greatest rate of elongation no doubt varies from stipe to stipe but frequently seems to be at about 5 cm from the apex. Table 2 shows that the apical 5 cm of stipe may more than treble its length in 14 days, while Table 5 reveals that over a period of 126 days a stipe may increase in length at an average rate of at least 3.4 cm per day.

TABLE 5

RESULTS OF TAGGING STIPE 10, 20, 30, 40, 50, 60, AND 100 CM FROM APEX, 17.ii.1950

Original Tagged Interval (cm)	Length of Interval After 46 Days (cm)		Length of Interval After 126 Days (cm)	
	Stipe 1	Stipe 2	Stipe 1	Stipe 2
Apex-10	149	156	247	335 (apex absent)
10-20	34	37	39	53
20-30	25	25	29	31
30-40	19	21	22	25
40-50	17	15	18	18
50-60	12	16	14	19
60-100	50	50	50	55

(*b*) *Age of Stipe*

It was found possible to pull a few small holdfasts, with the stones to which they were attached, into the boat and all the stipes of these plants were tagged 10 cm from the apex. Being comparatively loosely anchored, most of these plants were lost in storms but one was recovered on three occasions, when stipes already tagged were measured and any newly developed stipes were tagged. These measurements indicate that the rate of elongation in a young stipe is slow until it reached a certain length, which varies from stipe to stipe but is often between 30 and 60 cm. From this point increase in length takes place rapidly and there appears to be no marked reduction in the rate until the stipe approaches the end of its actively growing period and finally begins the formation of a bladder at the base of the terminal blade.

From observations made on this and other holdfasts it appears that the life of a stipe in the sheltered fringing beds varies generally between 7 and 10 months though maturity may be reached in a considerably shorter time.

TABLE 6

RESULTS OF TAGGING STIPE 10, 20, 30, 40, 50, 60, 100, 200, AND 300 CM FROM APEX, 17.i.1951

Original Tagged Interval (cm)	Length of Interval After 35 Days (cm)	
	Stipe 1	Stipe 2
Apex-10	56	Apex absent
10-20	19	24
20-30	13	18
30-40	12	15
40-50	11	15
50-60	11	10
60-100	47	40
100-200	—	108
200-300	—	100

(*c*) *Production of Blades*

It has been found by numerous taggings at various times during the year that the average rate of production of new blades on stipes of plants in sheltered localities is frequently in the vicinity of one every second day. However, the rate is very variable and production at the rate of one every day has been found on several occasions.

TABLE 7

GROWTH OF DETACHED TERMINAL BLADE WITH 10 CM OF STIPE

Initial No. of Blades in Detached Portion	Length of Detached Portion After 14 Days (cm)	Length of Detached Portion After 59 Days (cm)	Increase in No. of Blades After 14 Days	Increase in No. of Blades After 59 Days
27	11	—	3	—
22	12	—	1	—
18	11	—	2	—
26	12	37	3	13
23	10	—	1	—
25	11	—	0	—
25	11	30	2	10

Though not an infallible guide, the number of blades being initiated in the apical 5 or 10 cm of stipe is frequently a rough indication of the rate of growth of the stipe, a large number of blades indicating a rapid rate of elongation.

(*d*) *Growth of Detached Apices*

Terminal blades with a given length of adjacent stipe were severed and re-attached to the parent stipe with rubber bands. The growth of those of the detached portions which were recovered is shown in Tables 7-11.

TABLE 8

GROWTH OF DETACHED TERMINAL BLADE WITH 20 CM OF STIPE

Length of Detached Portion After 14 Days (cm)	Length of Detached Portion After 59 Days (cm)	Increase in No. of Blades after 14 Days	Increase in No. of Blades after 59 Days
24	—	1	—
20	—	0	—
22	—	0	—

These results indicate that the length of the detached portion of stipe with its apical blade seems to influence the growth rate of pieces up to 50 cm in length, beyond which it seems to have little effect.

TABLE 9

GROWTH OF DETACHED TERMINAL BLADE WITH 50 CM OF STIPE

Length of Detached Portion After 14 Days (cm)	Length of Detached Portion After 59 Days (cm)	Increase in No. of Blades after 14 Days	Increase in No. of Blades after 59 Days
63	305	3	55
78	290	—	—
78	300	6	52
65	257	2	44
67	—	8	—
63	—	4	—
60	287	4	54

(*e*) *Growth of Stipe with Defoliated Apical Region*

All blades and bladders were removed for a distance of 100 cm from the position of the fifth split in the apical blade. Most groups of stipes treated in this way were not recovered but of one group of 11, eight were recovered after 17 days. Of these, two lacked terminal blades, while one possessed a normal and apparently active terminal blade.

This suggests that the apical region is dependent to a considerable extent upon the blades immediately below it, though the results are not sufficient to draw definite conclusions. However, it must be remembered that, lacking bladders on adjacent parts of the stipe, the terminal blades drooped much further beneath the surface than normal, and this may have been at least partly responsible for the poor growth displayed.

TABLE 10

GROWTH OF DETACHED TERMINAL BLADE WITH 30 CM OF STIPE

Length of Detached Portion After 14 Days (cm)	Length of Detached Portion After 59 Days (cm)	Increase in No. of Blades after 14 Days	Increase in No. of Blades after 59 Days
36	196	0	31
33	210	0	25
34	186	0	35
41	179	3	35
34	192	0	26
35	—	0	—
38	180	2	32

(*f*) *Growth of Stipe with Apex Removed*

The apical portions of stipes were removed both at the position of the youngest and of the fifth split in the terminal blade and tags were attached at 30 cm and 100 cm from the position of severance. Only one stipe in which the apex had been removed at the position of the youngest split was recovered, but several of the second group were found and in neither was there any increase in the number of blades between the tag at 30 cm and the point of severance. This indicates that in the absence of the terminal blade the newly initiated blades cannot normally continue the growth by undergoing asymmetric splitting. After the maturation of the parts already laid down, growth in length practically ceases, and in 91 days the 30-cm interval from tag to point of severance increased to between 59 and 128 cm. This compared unfavourably with an increase in

TABLE 11

GROWTH OF DETACHED TERMINAL BLADE WITH 100 CM OF STIPE

Length of Detached Portion After 14 Days (cm)	Length of Detached Portion After 59 Days (cm)	Increase in No. of Blades after 14 Days	Increase in No. of Blades after 59 Days
143	304	5	66
141	—	9	—
144	304	6	66
138	—	5	—
134	300	6	58
134	314	9	61
121	264	4	53

the apical 30 cm in uninjured plants of 250-300 cm in 93 days. Table 12 shows the increase in length of stipes with apices removed at the position of the fifth split.

(*g*) *Growth of the Blade*

To measure the rate of growth and fix the position of meristematic activity a line of holes 3 cm apart was made along the junction of bladder and blade. Blades at 10, 20, 30, 40, and 50 cm from the apex were treated in this way and after a given period the distances between the holes were measured. Tables 13 and 14 give the results of these measurements made on one of the plants. Plate 4 shows the appearance after 9 days of blades punched with a series of holes 2 cm apart, the blades being located at the time of punching at 5, 10, 30, and 60 cm respectively from the apex.

TABLE 12

GROWTH OF STIPES WITH APICES REMOVED AT POSITION OF FIFTH SPLIT

Original Tagged Interval (cm)	Length of Interval After 91 Days (cm)					
	Stipe 1	Stipe 2	Stipe 3	Stipe 4	Stipe 5	Stipe 6
Apex-30	59	79	103	100	125	128
30-100	100	—	—	90	112	105

TABLE 13

GROWTH OF BLADES DURING 46 DAYS

Distance of blade from apex at time of punching (cm)	10	20	30	40	50
Increase in length due to growth after 46 days (cm)	62.5	49.4	29.6	21.4	9.6
Decrease in length due to decay at apex of blade after 46 days (cm)	0.4	8.5	11	3	13.1
Net increase or decrease in length of blade after 46 days (cm)	+62.4	+40.9	+18.6	+18.4	−3.5

Tables 1-14 allow of the following quantitative interpretation.

(1) The number of blades on the plant bears a linear proportion to the length of the stipe, this length (cm) being roughly 3.7 times the number of blades. In older plants (black dots in Fig. 8) blades may have been lost.

(2) The average growth increment, starting with a total length of 10 cm, appears to be in the first 30 days no growth, from 30 to 60 days 75 cm, from 60 to 90 days 75 cm, and from 90 to 120 days 160 cm (Fig. 9).

(3) The daily increment decreases logarithmically with the distance from the apex (Fig. 10). In late spring this relation seems to be least

pronounced. van Overbeek (1940*a*, 1940*b*) found the highest auxin activity in *Macrocystis pyrifera* in the terminal blade, the region of most rapid growth.

(4) Figure 11 shows the total increment of blades in 46 days. Here growth appears to be inversely proportional to the distance from the pneumatocysts. The curved lines in the diagram indicate regions of equal increment. van Overbeek found very little auxin in the pneumatocysts, still their influence on the growth of the blade cannot be denied. Owing to the variations in the seasons the total growth curve of the plant cannot be constructed.

TABLE 14

GROWTH OF BLADES DURING 46 DAYS

Distance of Blade From Apex at Time of Punching (cm)	Increase in Interval Between Bladder and First Hole, and Between Adjacent Holes from Base to Apex (cm)
10	56, 5, 1.3, 0.2, 0, 0
20	28.5, 13.8, 4.3, 1.4, 0.9, 0.3, 0.2, 0, 0, 0
30	12, 6.1, 5.5, 3, 1.8, 0.8, 0.2, 0.1, 0.1, 0, 0, 0, 0, 0
40	6.8, 3.9, 3.5, 2.8, 1.4, 0.9, 0.5, 0.2, 0, 0.2, 0.1, 0.1, 0.1, 0.2, 0.1, 0.2, 0, 0.1, 0.2, 0.2
50	2.1, 2.1, 1.7, 1.1, 0.6, 0.5, 0.3, 0.2, 0, 0.1, 0, 0, 0.1, 0, 0, 0, 0.2, 0.1, 0.2, 0, 0, 0.2, 0.1

The results of these and other measurements indicate that the greatest meristematic activity is located at the base of the blades in the 3 cm above the junction with the bladder and that this activity rapidly decreases upwards. The most rapid increase appears to take place in blades located at some point generally between 5 and 10 cm from the apex. Behind this point the rate of elongation decreases and a blade reaches maturity at some point between 30 and 100 cm from the apex, usually taking between 2 and 3 months from the date of initiation. The lateral blades when freed from the terminal blade generally carry away a small part of the terminal blade at their apex but this is fairly soon shed. Decay or wear sometimes appears early at the apex of a blade though for a time the loss here is more than made good by the increases resulting from meristematic activity at the base of the blade. A point is finally reached where loss from decay exceeds the increase at the base and from that point onwards the length of the blade decreases as it decays progressively downwards until even the bladder rots away, leaving the stipe quite bare. In long stipes, frequently only a small proportion of the length carries bladders and blades, the rest carrying only the stumps of bladder stalks (Plate 1, Fig. 1). There seems to be considerable variation in the length of life of a blade but generally after 4 months from the date of initiation at least half of the blade has decayed.

VIII. Harvesting

Experimental harvests were made at Triabunna, Port Arthur, and Hythe (Southport). In each of these localities a fringing kelp bed which appeared to be of average density was chosen for the trial. A plot 20 or 30 m square was marked out from the shore by lines and the positions of the outer corners fixed by danbuoys. Paint marks were made on rocks on the shore so that the same area could readily be marked out again at a subsequent date.

Within this area all kelp was cut at approximately 3 ft below the surface of the water, using reaping hooks which had been further bent and attached to handles about 6 ft long. Kelp in a strip 10 ft wide bordering the plot was also cut but not measured so that at a subsequent harvest there would be no possibility of kelp from unharvested areas outside the plot being carried by the tide into the harvest area. Where possible all the stipes from one holdfast were gathered together and the mass was then cut and drawn into the boat. Indiscriminate slashing of the stipes and subsequent collection of the pieces was a slower method and had the added disadvantage that many smaller pieces were carried away by the tide before they could be lifted out on the hooks (Plate 3, Fig. 1). One man working from a boat was sometimes able to tie a rope round a group of stipes which he then cut while a second man on the shore pulled the mass to the bank. Where there was little swell on the shore this method was often less awkward than loading the heavy weed into a boat.

Table 15
RESULTS OF TRIAL HARVESTS AT PORT ARTHUR

Date of Harvest	Quantity Harvested (lb)	Yield (tons/ac)
2.ii.1950	2640	5.7
19.vi.1950	3726	8.0
13.ix.1950	1564	3.4
23.i.1951	897	1.9
19.vi.1951	1955	4.2
29.x.1951	1932	4.2
12.i.1952	1495	3.2

After the kelp had been either dragged ashore or loaded into the boat it was measured by packing into a wooden box, the average filled weight of which was known from numerous weighings with a spring balance.

The boats used were either rowing or motor dinghies varying from 8 to 20 ft long. The 8-ft dinghy was too small and unstable, carrying only one man and a comparatively small load of kelp, but a 16-ft motor dinghy used at Port Arthur was more satisfactory as this could carry two or three men with a load of 600 lb of kelp, and could be used when the sea was not entirely calm. This and smaller boats had the advantage that they could be manoeuvred slowly by paddling with the harvesting hooks whereas larger craft could be moved only by oar or engine. Larger boats were also inconvenient in that it was more difficult to lift the heavy mass of kelp over the higher sides.

These harvests were carried out on the narrow fringing beds in comparatively sheltered situations where the depth did not exceed 20 ft. Commercial harvests would be made over the larger beds of vigorous kelp in more exposed waters but in such positions some distance from the shore it was impossible to carry out repeated experimental harvests over the same small area, and it is assumed that growth rates and regeneration in these areas are at least as good as in the sheltered positions where harvests were made. Rapson, Moore, and Elliott (1943) pointed out that these plants in deeper water must produce a greater length of new stem than those in shallow water before the stems reach the surface for a second cutting, and they suggest that this may be compensated for by faster growth at deeper levels. This accelerated growth may occur, but though there may be some rhythm in the production of new stipes, there appear generally to be stipes in all stages of development on a given plant and, at least in deeper water, it is probably those young stipes just out of reach of the harvesting knives rather than the youngest stipes near the holdfast which will provide the bulk of the subsequent harvest, so that even if growth rate does not vary in the manner suggested it seems unlikely that the frequency of possible harvests will be reduced with increasing depth of holdfast attachment.

TABLE 16

RESULTS OF TRIAL HARVESTS AT TRIABUNNA

Date of Harvest	Quantity Harvested (lb)	Yield (tons/ac)
18.iii.1950	2990	7.0
21.vi.1950	1127	2.6
11.ix.1950	736	1.7
25.i.1951	253	0.6
11.vi.1951	230	0.5
8.x.1951	1840	4.3
23.i.1952	690	1.6

The plots were harvested three times a year and though it has been noted that the heaviest growth of kelp is generally to be seen during the winter months, roughly between May and September, the harvest figures do not clearly show this trend, largely because of the storms which at any time of the year may overnight reduce the possible yield of a bed to only a small fraction of its previous value.

The density of kelp within the harvest plot has on each occasion immediately prior to harvesting appeared equal to that in surrounding areas, and over the 2 yr of the experiment there has been no indication that harvesting at approximately 4-monthly intervals has had any adverse effect on the bed.

After allowance had been made for the strip of shallow water near the shore not colonized by *Macrocystis,* the effective areas harvested were 840 sq. m. at Port Arthur, 780 sq. m. at Triabunna, and 360 sq. m. at Hythe (Southport).

The results of the harvests are given in Tables 15-17. At Hythe, sand encroached over the rocky bottom of the bed during the latter part of 1950, causing the disappearance of part of the *Macrocystis,* and for this reason figures for only the first two harvests are given.

The average yield obtained was 4 tons/ac and the maximum yield 12.2 tons/ac at Hythe (Southport).

TABLE 17
RESULTS OF TRIAL HARVESTS AT HYTHE
(SOUTHPORT)

Date of Harvest	Quantity Harvested (lb)	Yield (tons/ac)
22.iii.1950	2415	12.2
20.vi.1950	598	3.0

It probably would be unprofitable to harvest at depths greater than 3-4 ft. Below this level the mature stipes carry a decreasing proportion of healthy blades and bladders, and cutting the apices of young stipes would destroy part of the potential subsequent crop for an insignificant increase in immediate yield.

A swiftly running tide or rough sea frequently carries the stipes some distance below the surface, making them unavailable for cutting, and commercial harvesting could be carried out only during fairly calm weather.

Cameron (1915) gives descriptions and illustrations of a mechanical harvester with a probable capacity, if run steadily in medium or heavy kelp beds, of 25 tons/hr or more of fresh kelp.

After severe storms, great tangled masses of *Macrocystis* (Plate 2, Fig. 1) often lie half buried along the sandy beaches, but though the quantities are often considerable, their irregularity of occurrence, inaccessibility, contamination with sand, and difficulty of collection render them of little significance from a commercial point of view.

IX. DRYING OF MACROCYSTIS

When drying *Macrocystis* in quantity it has been found advisable to leave the freshly cut kelp lying on the shore for a day to allow excess water to drain away. The lightened mass is then spread over wire lines or poles as shown in Plate 3, Figure 2. If the kelp has been spread thinly and the weather is warm and sunny, drying may be completed in 3 days or during exceptionally good weather within 2 days. But showery weather, particularly when occurring during winter months, keeps the kelp in a moist state often for several weeks, and the mass must be frequently turned to avoid rotting.

TABLE 18

RESULTS OF SURVEY IN THE VICINITY OF TRIABUNNA

Sub-area	Area (ac)	Tonnage Calculated at 4 Tons/ac
Grindstone Bay	5,040	20,160
Cape Bouganville (North)	3,200	12,800
Oakhampton Bay	400	1,600
Home-lookout Point	128	512
Windlass Bay	96	384
Johnstone Point (South)	640	2,560
Macquarie Reef	139	556
Stapleton Point	111	444
Meredith Point	10	40
South of Oyster Bay, Maria I.	430	1,920
Oyster Bay, Maria I.	2,560	10,240
North of Oyster Bay, Maria I.	1,504	6,016
Total	14,308	57,232

X. SURVEY

The width of narrow fringing beds at Port Arthur was measured generally by sailing along the outer edge of a bed and throwing a weighted marked line to the shore at regular intervals. In a few places, where the nature of the shore permitted, the line was stretched between one man in the moving boat and another walking along the shore. The length of the bed was measured by means of a range-finder.

Where larger areas were involved danbuoys were placed at various points on the margin of the beds, compass bearings were taken on these points, and the distance between the danbuoys measured by rangefinder.

The areas of the beds surveyed together with the estimated possible harvest calculated on the basis of the average of 4 tons/ac are given in Tables 18-21. The distribution of these beds is shown in Figures 12-16.

As can be seen from these figures, by far the largest beds are located in the vicinity of Triabunna and Actaeon I.

On the basis of an average yield of 4 tons/ac and three harvests per year the beds surveyed could be expected to yield approximately 355,000 tons of wet weed per year, or, since 1 ton of air-dried weed is obtained for 8-10 tons of wet weed, between 35,000 and 44,000 tons of air-dried weed per year. If, as the analyses indicate, the average alginic acid content is approximately 21 per cent. on a dry weight basis, the annual alginic acid resources would be of the order of 7,000-9,000 tons. However, it must be recognized that these figures have been arrived at by including the experimental harvests from beds recently denuded by storms. If commercial harvesting were undertaken it is likely that beds would be harvested immediately on reaching maturity and the loss from storms would be very much reduced, so that the estimate of 355,000 tons of wet weed per annum is probably a conservative one, and it is likely that a quantity in excess of this could be harvested during many years.

TABLE 19

RESULTS OF SURVEY AT PORT ARTHUR

Sub-area	Area (ac)	Tonnage Calculated at 4 Tons/ac
Opossum Bay	3	12
Frying Pan Point	3	12
North shore of Frying Pan Point	1	4
Stewarts Bay to Garden Point	2	8
Garden Point to Stingray Bay	10	40
Eastern shore of Long Bay	7	28
Evidence Point to Stinking Beach	7	28
Stinking Beach to Denmans Bay	27	108
Dead I. and Point Puer	33	132
Safety Cove	206	824
Half Moon Bay	14	56
Total	313	1,252

TABLE 20

RESULTS OF SURVEY AT BRUNY I.

Sub-area	Area (ac)	Tonnage Calculated at 4 tons/ac
Pearson's Point to Blackmans Bay	40	160
Kelly's Point	10	40
Kelly's Point to Cape de la Sortie	24	96
Cape de la Sortie across Bull Bay	160	640
One Tree Point	9	36
Trumpeter Bay	36	144
Yellow Bluffs	1	4
Variety Bay	96	384
South of Cape Connella	40	160
Adjacent Arched I.	30	120
Total	446	1,784

XI. ANALYSIS OF MACROCYSTIS

Monthly samples of *Macrocystis* obtained from Triabunna and Port Arthur were analysed for alginic acid and mannitol content. However, the inadequate method of sampling and inconsistent drying procedure render the results of reduced value. The analyses (Table 22) were carried out by the method outlined by Cameron, Ross, and Percival (1948).

TABLE 21

RESULTS OF SURVEY IN THE VICINITY OF ACTAEON I.

Sub-area	Area (ac)	Tonnage Calculated at 4 tons/ac
Actaeon I.	10,560	42,240
Sullivan's Point	682	2,728
Southport I.	240	960
Eel Point to Fishery Point	142	504
Fishery Point	126	568
Dead I.	6	24
Sullivan's Point to Black Reef	320	1,280
Mutton Rocks to Sullivan's Point	533	2,132
Blind Reef to Recherche Bay	480	1,920
Recherche Bay	1,440	5,760
Total	14,529	58,116

Sannie (1950) reported the alginic acid content for a sample of *Macrocystis pyrifera* from Kerguelen as 17.65, 18.79, and 20.94 per cent. for fronds, stipes, and bladders respectively, and the mannitol content as 4.15, 5.78, and 6.07 per cent. respectively. According to Chapman (1950), Lund found an alginic acid content of 14-18.7 per cent., and Hoagland (1915) reported 16.2 per cent. algin in blades and 18.2 per cent. in stipes.

TABLE 22

ANALYSIS OF MACROCYSTIS

Locality	Date	Alginic Acid (%)	Mannitol (%)
Triabunna	October 1950	23.19	9.11
Port Arthur	October 1950	25.61	7.34
Triabunna	November 1950	17.15	11.55
Port Arthur	November 1950	29.36	8.91
Triabunna	December 1950	15.22	9.68
Port Arthur	December 1950	21.09	10.41
Port Arthur	January 1951	20.29	8.94
Triabunna	January 1951	20.78	8.48
Port Arthur	February 1951	16.19	6.06
Port Arthur	March 1951	20.78	8.48
Port Arthur	April 1951	22.09	9.46
Port Arthur	May 1951	24.19	6.83
Port Arthur	August 1951	22.22	7.55

No estimations of potash content have been made, but numerous authors, particularly in America, have dealt with this aspect of the investigation. Burd (1915) gave an average potash (K_2O) content of 13.6 per cent. for *Macrocystis pyrifera* on the Pacific coast of North America while Cameron (1915) found the potash content varying between 3.10 and 27.66 per cent., with an average of 12.59 per cent. Rapson, Moore, and Elliott (1943) in New Zealand reported that, except in drift samples, the potassium chloride content is more than 23 per cent. Burd (1915) shows a greater proportion of potash in stipes than in blades.

XII. CONCLUSIONS

The results of these investigations seem to indicate that a probable minimum of 35,000-44,000 tons of air-dried weed could be obtained in three harvests per year from nearly 30,000 ac of *Macrocystis* beds surveyed.

TABLE 23

AVERAGE MONTHLY RAINFALL (POINTS)

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Triabunna	161	214	281	249	168	292	195	161	155	252	194	302	2624
Hythe	278	217	309	338	309	361	344	354	315	369	307	295	3796

If an industry should be established it would probably be best situated near either Triabunna or Hythe, the towns nearest to the large beds of *Macrocystis*. For the production of alginic acid, the weed could be treated shortly after harvesting, but it would be advisable to build up a supply of dried weed so that there would be no necessity to cease production in the event of a shortage of fresh kelp caused by either destruction of the beds during storms or poor growth due to unusually warm water temperatures. If the availability of facilities for air-drying of the weed is to be an important consideration in the choosing of a site for operations, Triabunna, with a much smaller rainfall than Hythe, might have preference over this latter locality. The average monthly rainfalls for these two localities are shown in Table 23. Triabunna is also favoured in that Maria I. affords considerable shelter to beds in the vicinity.

XIII. ACKNOWLEDGMENTS

The author wishes to express his thanks to Professor L. Newton, Department of Botany, University College of Wales, Aberystwyth, and to Mr. E. J. F. Wood* for advice and suggestions during the course of the investigation, to Mr. E. J. F. Wood for permission to use the results of the survey and analyses, which were carried out under his direction, and to Professor L. Newton; Dr. H. Thompson, Chief of the Division of Fisheries; and Mr. E. J. F. Wood for suggestions made during the preparation of the paper. The author also gratefully acknowledges the valuable suggestions for the improvement of the manuscript made by Professor L. G. M. Baas Becking, who prepared Figures 8-11.

Mr. L. H. Crosby* performed nearly all the work connected with the surveying and subsequent mapping of the *Macrocystis* beds, Mr. C. R. Purday* carried out the analysis of the *Macrocystis* samples, and Mr. R. Breach* prepared the maps and the prints of all photographs appearing in the paper, and photographed the specimens appearing in Plate 1, Figure 2, and Plate 4.

To Mr. D. Martin, Officer in Charge of the C.S.I.R.O. Regional Laboratory, Hobart, and to other members of the staff of the laboratory, thanks are due for providing facilities for work during visits to Tasmania.

The author is also greatly indebted to Mr. E. J. Wenck of Port Arthur, who rendered valuable assistance in the field and gave freely of his knowledge of local conditions.

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MACROCYSTIS PYRIFERA IN TASMANIA

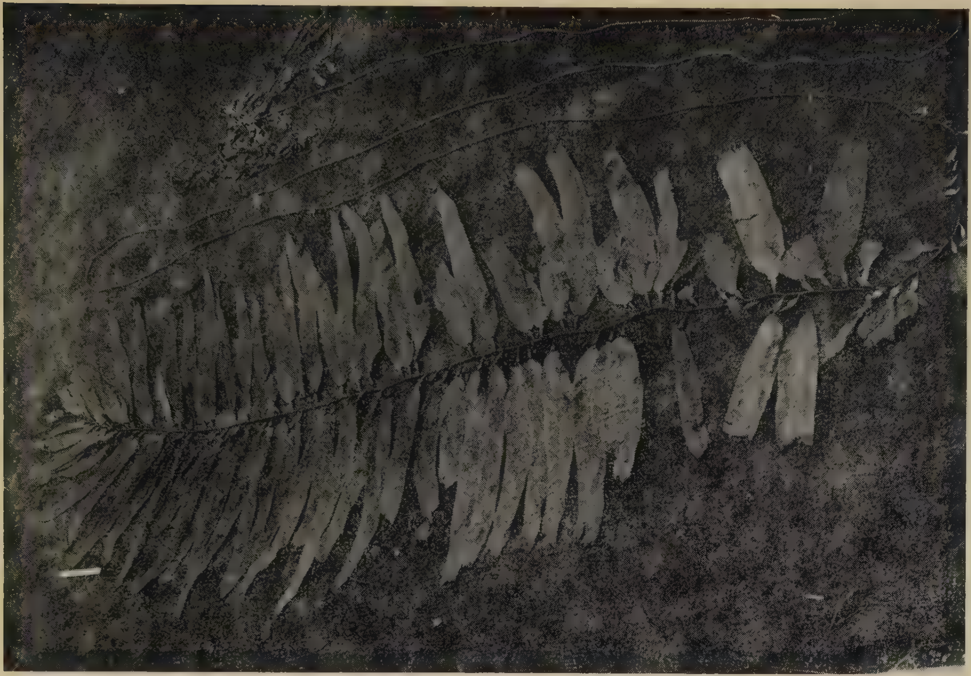


Fig. 1.—A *Macrocystis* stipe 65 ft long spread out on ground; a foot rule appears in the lower left-hand corner.

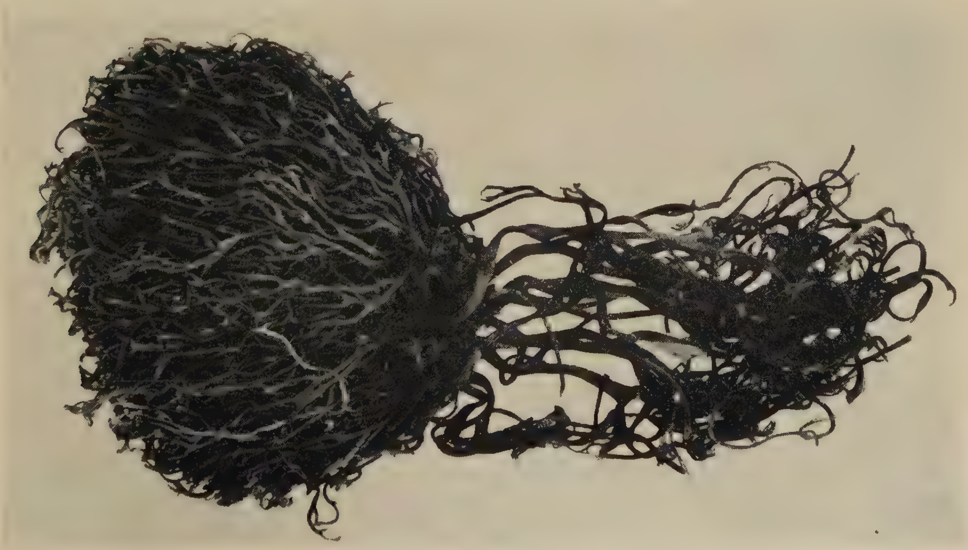


Fig. 2.—Holdfast of *Macrocystis pyrifera* occurring on the east coast of Tasmania.

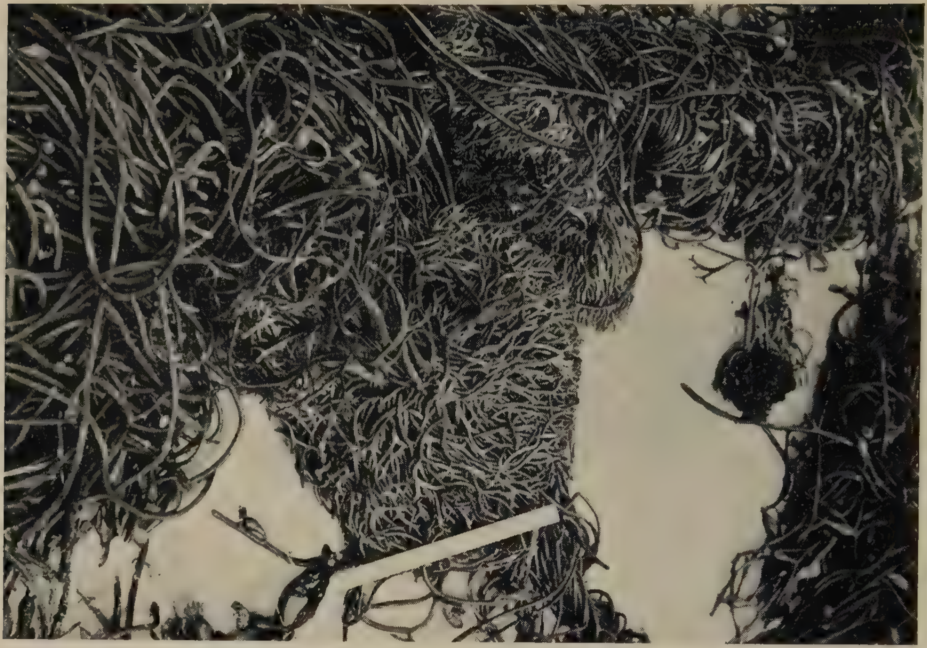


Fig. 1.—Holdfasts and tangled stipes of drift *Macrocystis pyrifera.*

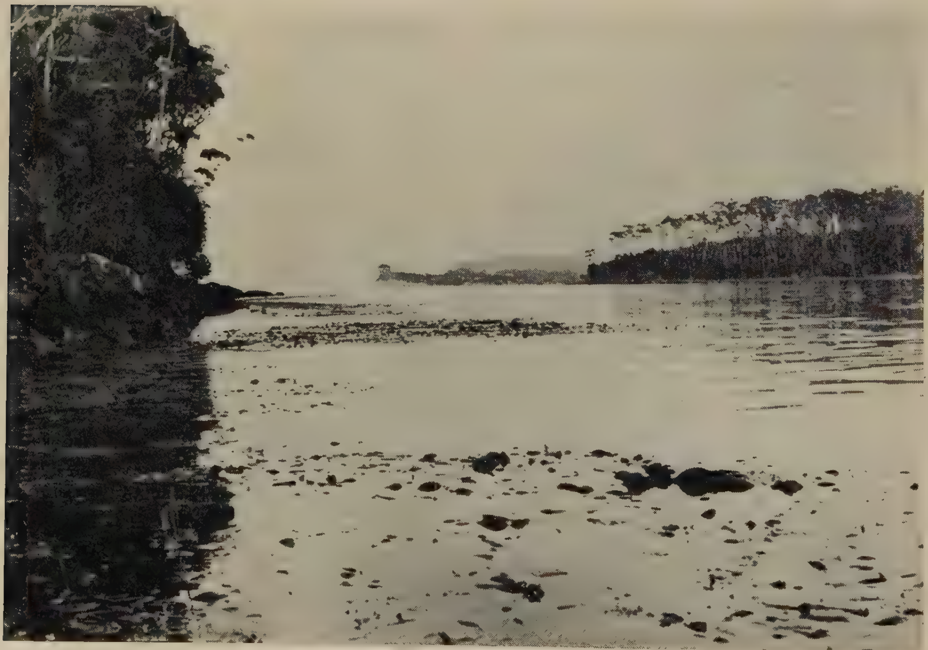


Fig. 2.—Narrow fringing bed of *Macrocystis pyrifera* at Port Arthur.

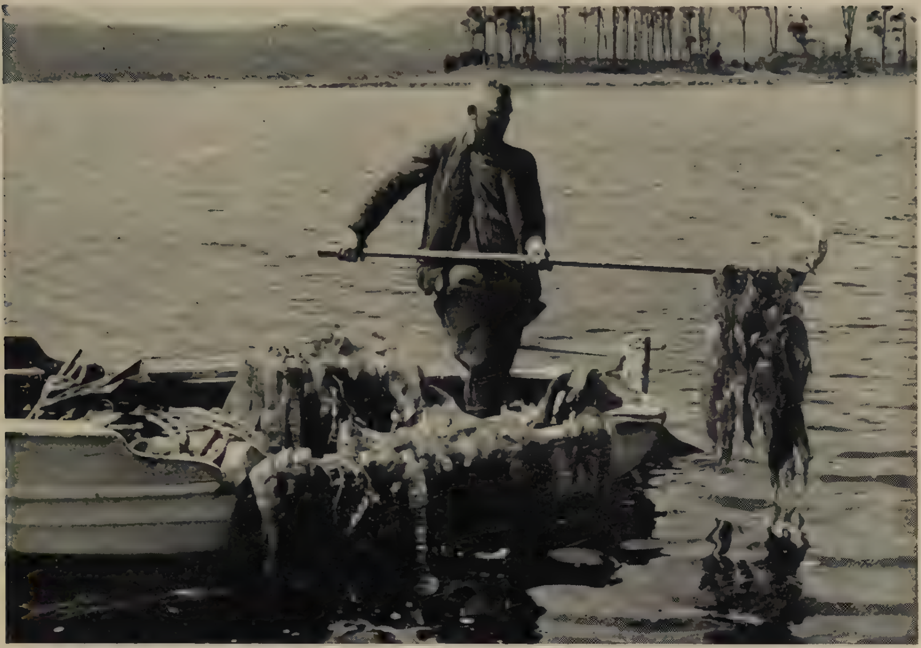


Fig. 1.—Harvesting *Macrocystis pyrifera* at Port Arthur.

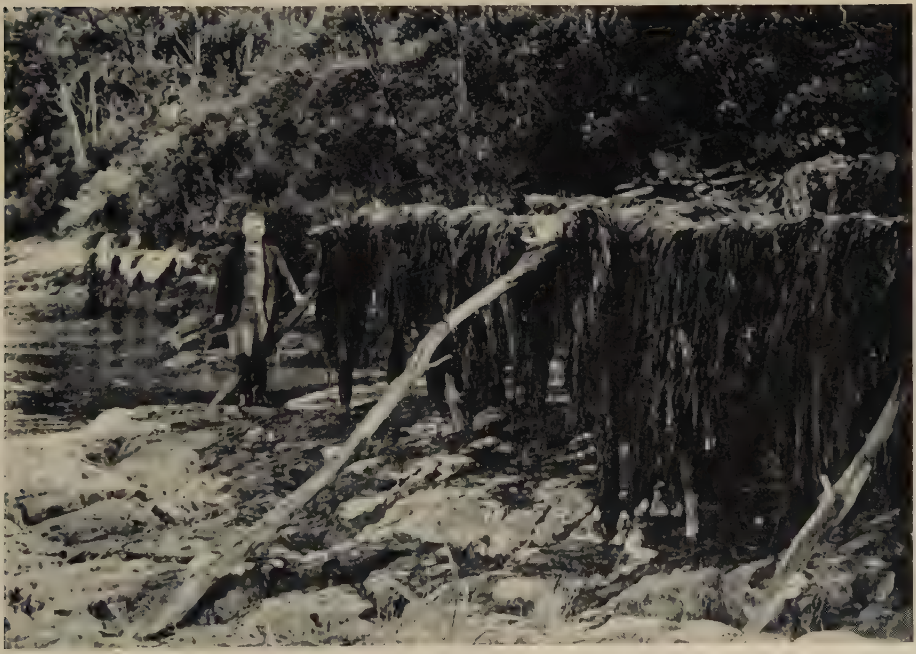
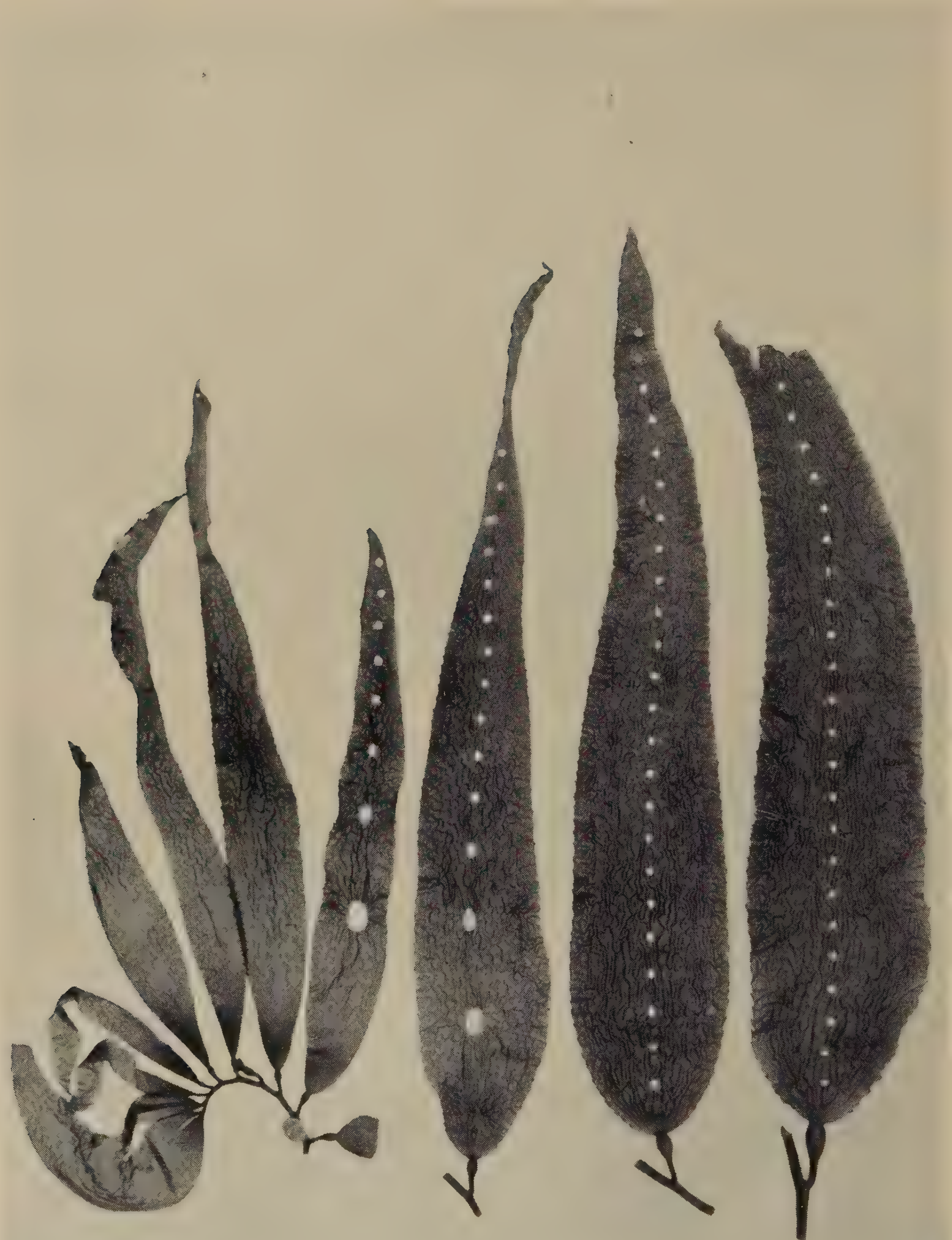


Fig. 2.—Drying *Macrocystis pyrifera* at Port Arthur.

MACROCYSTIS PYRIFERA IN TASMANIA



Blades 9 days after punching a row of holes 3 cm apart, the blades then being located at 5, 10, 30, and 60 cm respectively from the apex.

STUDIES ON THE OVARIES OF THE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE), ON THE WESTERN AUSTRALIAN COAST

By R. G. Chittleborough*

(*Manuscript received October* 19, 1953)

Summary

Observations on the increase of ovarian weight in the female humpback whale cover stages from late foetal life until after the attainment of sexual maturity. Variations in ovary weight during different phases of the reproductive cycle are recorded.

Graafian follicles up to 0.13 mm in diameter have been found in the foetal ovary just prior to birth. These initially develop until from 11 to 29 mm (median value 20 mm) in diameter when the female reaches the maturing length range. At sexual maturity one of these follicles enlarges, exceeding 30 mm in diameter before rupture. After ovulation a corpus luteum is rapidly formed and if conception has taken place, this gland enlarges and remains active until parturition. After parturition there is rapid resorption of the corpus luteum to form a corpus albicans. Variations in the sizes and weights of functional corpora lutea are discussed.

There is considerable reduction in the diameters of Graafian follicles in late pregnancy to a median value of 6 mm. After parturition follicles enlarge so that in the ovaries of females in late lactation the largest follicles once more range from 11 to 29 mm in diameter with a median value of 20 mm.

In an ovulatory period of from June to November the maximum frequency of ovulations is in late July, though considerable numbers occur in August and September. On the available evidence most female humpback whales ovulate only once in their ovulatory period, a few ovulate twice, and extremely few three times.

I. INTRODUCTION

Observations upon the ovaries and a consideration of the reproductive cycle of the female humpback whale (*Megaptera nodosa* (Bonnaterre)) are recorded by Matthews (1937) in his general report upon humpback whales from the South Atlantic Ocean. Ovary weights were then available from very few females and, as Matthews indicated, these records were insufficient for detailed analysis. He pointed out that ovary weight increased at sexual maturity and assumed that this increase continued thereafter with some decrease in old age. With many more records of ovary weight, a more detailed analysis of such variations can be made.

Matthews referred to the enlarging of Graafian follicles at the approach of ovulation, saying that such follicles project further from the surface of the ovary, but gave no actual measurements.

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* Western Australian Branch Laboratory, Division of Fisheries, C.S.I.R.O., University of Western Australia, Nedlands, W.A.

The size and weight of some functional corpora lutea were given in that report (Matthews 1937, p. 60) and the general statement was made that corpora lutea of pregnancy shrink rapidly after parturition, but the data were insufficient to analyse the variation in corpus luteum size at the different stages and the rate of resorption after parturition. Matthews distinguished the corpus luteum *"a"* (active) from the corpus luteum *"b"* (really a corpus albicans), stating that the transition was gradual. The present paper does not follow this designation but shows that after parturition the transition from an active corpus luteum (corpus graviditatum) to a corpus albicans is a rapid process.

From an analysis of foetal length Matthews concluded that the frequency of pairing was greatest between August and November with highest intensity in September. Using 11 months as the gestation period, he then indicated that the maximum frequency of births occurred in August. He stated that at birth calves were 4.5-5 m in length.

From the evidence available to him, Matthews concluded that the species bred once every 2 yr but that two pregnancies might sometimes occur in 3 yr; the much greater evidence now adduced supports this view. This evidence is based upon data gathered by the author at shore stations on the Western Australian coast in 1951 and 1952, supplemented by material collected by Whaling Inspectors of the State Fisheries Department from 1949 to 1952. The material from the three Western Australian whaling stations (at Point Cloates, Carnarvon, and Albany) for different years has been considered together.

This paper is mainly concerned with the macroscopic features of the ovaries and of the changes taking place in development from the late foetal stage until maturity, together with changes during the reproductive cycle. Considerable information concerning the time and frequency of ovulation has been acquired from the examination of over 300 pairs of ovaries from sexually mature females.

II. METHODS

Ovaries were examined as follows: after a superficial examination the whole ovary was sectioned transversely, using a meat slicer set to give sections of approximately 5 mm in thickness. It is considered that in this way no corpus albicans, however slight its remains may be, can be missed. Slices so taken are illustrated in Plates 2-6.

In these instances, as a result of prolonged immersion in formaldehyde solution, the follicular fluid had gelatinized and the tissues hardened, greatly assisting in the preparation of suitable slices for photography. Samples of foetal ovaries required for histological examination were fixed in Heidenhain's Susa fixative.

The results from the analysis of further ovarian material fixed for histological examination will be presented in a separate paper.

III. Ovary Weight

(*a*) *Foetal Ovaries*

In general appearance the ovaries of humpback whales in the late foetal stage were similar to those of blue and fin whales described by Mackintosh and Wheeler (1929, p. 383), having a deep red colour and a much wrinkled surface. Table 1 shows the weights of the ovaries and the body lengths of late foetal humpback whales. Three of these foetuses are within or above the length range at birth as found by Matthews (see above), and their respective total ovary weights were 56.5, 107, and 173 g. Thus the present range of total ovary weight just prior to birth is 56.5-173 g.

Table 1

OVARY WEIGHTS FROM LATE FOETUSES

Length of Foetus (m)	Weights of Ovaries (g)		Total Weight of Ovaries (g)
2.82	26	26	52
3.78	50	55	105
4.34	48	55	103
4.54	28	28.5	56.5
4.91	85	88	173
5.03	49	58	107

(*b*) *Immature Ovaries*

As shown in Figure 1, ovary weight increases very little until a body length of about 34 ft is attained (with the exception of one immature female 29 ft 3 in. long which had a total ovary weight of 580 g). As sexual maturity approaches, ovary weight increases, but at the same time there is a greater individual variation. The maximum recorded total ovarian weight in an immature female was 3425 g. This is exceptionally high, but these ovaries appeared to be otherwise normal.

Owing to the wide range of values (Fig. 1) just prior to and after sexual maturation, it is not possible to distinguish mature and immature females on a basis of ovary weight as done by Jonsgard (1951) for the minke whale. Matthews (1937) noted that immature humpback ovaries seldom exceed 1½ lb (682 g), but Figure 1 of this paper shows that in immature females close to maturity the total weight of the ovaries not infrequently exceeds this value.

(*c*) *Mature Ovaries*

Figure 1 suggests that the increase in ovary weight with body length begun shortly before sexual maturity continues to some extent after the attainment of sexual maturity, but here the range of values is very wide.

When ovary weight is plotted against the number of corpora lutea (as an index of relative age) as shown in Figure 2, there is little evidence of increased ovary weight with relative age in sexually mature females. Mackintosh and Wheeler (1929) suggested that in fin and blue whales there is a decrease in ovary weight in older females (having 13 and 20 corpora lutea), but Figure 2 does not indicate any marked decrease in

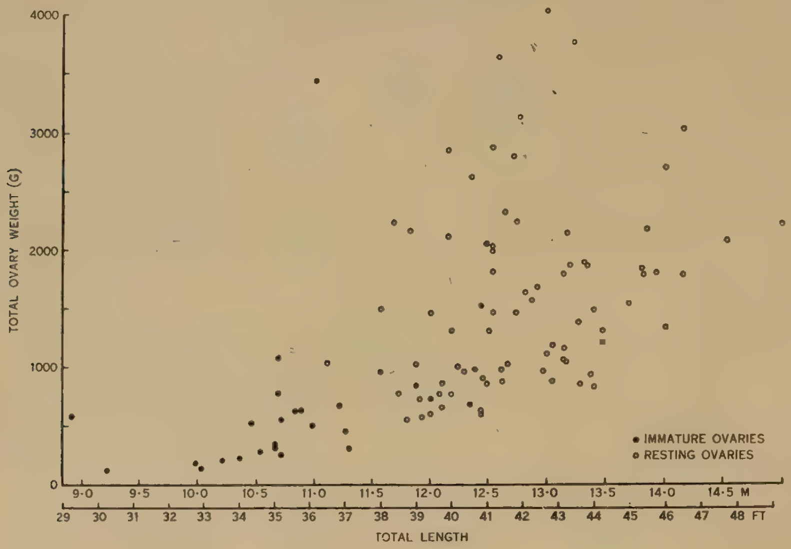

Fig. 1.—Total ovary weight and total length of females with immature and resting ovaries.

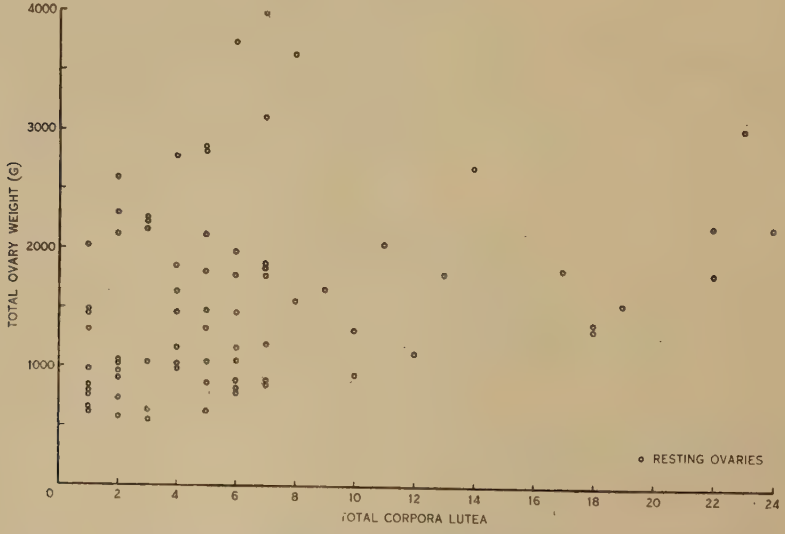

Fig. 2.—Total ovary weight and total corpora lutea of mature females with resting ovaries.

ovary weight of older female humpback whales having up to 24 corpora lutea in the ovaries.

The ovarian weights of mature females shown in Figures 1 and 2 are from ovaries in the resting phase, i.e. from females which were not pregnant, in the earlier stages of lactation, recently ovulated, or about to ovulate, so that possible variations in ovary weight within the reproductive cycle could be avoided in these figures. Ovaries of females in late stages of lactation are included in Figures 1 and 2 as these had all the features of resting ovaries; they possessed no corpus luteum showing signs of activity, and the Graafian follicles were of similar size to those in the ovaries of resting females (see Section IV (*e*) (iii)). The body length and total ovarian weight of each female shown in Figures 1 and 2 are listed in Appendix I.

TABLE 2

OVARY WEIGHTS AT VARIOUS STAGES OF THE REPRODUCTIVE CYCLE

Stage	Number of Females	Total Weight of Ovaries (g)				Weight of Single Ovaries (g)	
		Geom. Mean	Arith. Mean	Min.	Max.	Min.	Max.
Resting	20	1428	1547	625	2845	260	1525
Approaching ovulation	19	1322	1449	514	2400	184	1255
At ovulation	16	1033	1196	355	2795	160	1600
Early corpus luteum*	26	1378	1661	545	5505	172	2685
Late pregnancy	7	1992	2161	1120	3836	345	3204
Early lactation	5	1455	1624	845	3000	325	1845
Late lactation	56	1395	1590	550	3980	200	2095

* No embryo found but possibly some of these females may have just begun a pregnancy.

Table 2 shows the ranges of ovary weights of females in various stages of the reproductive cycle, together with the geometric and arithmetic means of paired ovary weights in the various stages. The distribution of ovary weights within each stage was unimodal and positively skewed so that for purposes of statistical analysis a logarithmic transformation was used to normalize the variation. The best estimate of the mean for each class is then found by working with transformed values, and this, in terms of the original data, corresponds to the geometric mean, which is used for the comparison of ovary weights in the stages shown in Table 2.

The above geometric means show little variation at the different stages, except that females which have just ovulated tend to have slightly lower total ovary weight, and females in late pregnancy a higher ovary weight than at other stages. But the range of values within all stages is so great that the differences in these geometric means are mostly not significant on the numbers of ovaries weighed. In the comparison of the geometric means of paired ovary weights in resting females and those at ovulation, by means of the t test, $t = 1.946$ on 34 degrees of freedom, which is not significant. Also in the comparison of the geometric means of paired ovary weights in resting females and those of late pregnant females, $t = 1.785$ on 25 degrees of freedom, which is not significant. However, in the comparison of the geometric means of paired ovary weights in females at ovulation and those in late pregnancy, $t = 2.677$ on 21 degrees of freedom, which is significant at the 2 per cent. level. The presence of a large functional corpus luteum in one ovary of each female in late pregnancy (weights of functional corpora lutea discussed under Section V (*b*)) tends to increase the total weight of the ovaries, although in late pregnant females the Graafian follicles are much reduced in size, as shown in Section IV (*d*).

IV. Graafian Follicles

(*a*) *Follicles in Late Foetal Calves*

Sections of ovaries from late foetal female humpback whales show oogonia gathered in cavities (Pflüger's tubes) immediately below the ovarian surface. Slightly deeper in the ovarian tissue primary oocytes are abundant, each ovum being surrounded by a single layer of epithelial cells (Plate 1, Figs. 1, 2). In one primary oocyte the single layer of epithelial cells enclosed three ova (Plate 1, Fig. 3).

The largest early Graafian follicles in late foetuses are deepest in the ovaries, up to 2.5 mm from the surface. Some of these (Plate 1, Fig. 4) reach 0.13 mm in diameter, having an epithelial layer up to three cells thick and traces of a zona pellucida visible.

(*b*) *Immature, Resting, and Maturing Follicles*

In the examination of over 400 sets of humpback whale ovaries it has usually been found possible to distinguish maturing or mature Graafian follicles from well-developed but resting follicles. In larger immature females, and also in mature females not in late pregnancy or early lactation and not about to ovulate, the largest follicles are well developed but resting. Though these follicles do not project to any great extent from the general ovarian surface, they are sufficiently close to the surface to be seen in whole ovaries as purplish areas.

As a Graafian follicle approaches maturity it enlarges, projecting further from the surface of the ovary than the resting follicles (see Plates 2 and 3). The follicle wall becomes thinner on the projecting surface and fine blood vessels become visible in the wall. Except in a few older females where some follicles have degenerated into cysts, Graafian follicles at or over 30 mm in diameter are maturing and females with such follicles are approaching ovulation.

Figure 3 shows the diameter of the largest follicle in the ovaries plotted against the length of the female, using only immature females and mature females which were not pregnant, lactating, or recently ovulated. Upon a superficial examination, Figure 3 would appear to verify the findings of Nishiwaki and Oye (1948, p. 119), and Nishiwaki and Hayashi (1950, p. 156), who claimed that in mature blue and fin whales the size of the largest Graafian follicle is in proportion to the body length. However, in the humpback whales shown in Figure 3, those whose largest follicle was less than 30 mm in diameter must be considered apart from those whose largest follicle exceeded 30 mm in diameter as these two groups represent separate physiological conditions, the first being in the resting (anoestrus) condition, and the second approaching ovulation (prooestrus).

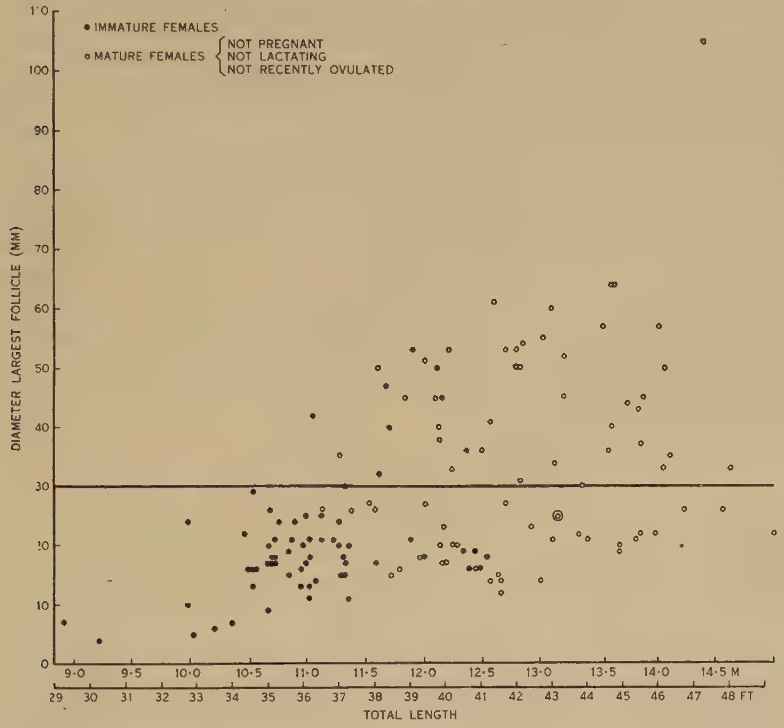

Fig. 3.—Diameter of largest Graafian follicle; immature and specified mature females.

Considering the immature females shown in Figure 3, those having a Graafian follicle at or over 30 mm in diameter are approaching their first ovulation. The shortest sexually mature female humpback whale found amongst Western Australian coast females was 35.5 ft long, while immature females up to 41.17 ft have been recorded. The immature females approaching their first ovulation (one Graafian follicle 30 mm or more in diameter) shown in Figure 3 are within this length range of 35.5-41.17 ft.

In the ovaries of immature females which are within this length range and have no maturing follicles, the largest Graafian follicle measured from 11 to 29 mm in diameter, with a median value of 20 mm. The upper sections in Plate 2 show the typical appearance across the ovaries of such an immature female.

Of the sexually mature females shown in Figure 3, the largest Graafian follicle in the ovaries of those which were not approaching ovulation measured from 12 to 28 mm in diameter, with a median value of 20 mm. Such females are classed in this report as resting or anoestrus females; they were not pregnant or lactating, had not recently ovulated, and were not approaching ovulation.

Figure 3 shows that some female humpback whales reach sexual maturity when between 36 and 39 ft long, while a number do not mature until from 40 to just over 41 ft. This may be due to different individual growth rates amongst females of the same age. Alternatively it is possible that this wide difference in lengths at sexual maturity may have resulted from some females reaching sexual maturity at 2 yr of age and others at 3 yr. The available records are only sufficient to suggest the possibility that some female humpback whales mature at 2 yr and others at 3 yr. In this regard Matthews (1937) suggested that sexual maturity was reached at 2 yr in humpback whales, but Mackintosh (1942) allowed the possibility of maturity being deferred until the third year in female humpback whales.

(*c*) *Ovulation*

Thirty-five of the female humpback whales examined on the flensing deck were found to have just ovulated, the blood-stained hole (from 4 to 13 mm in diameter) being immediately obvious on the surface of the ovary. When ovulation had occurred immediately prior to the death of the female and the ovary was then cut across the collapsed follicle the latter was found to contain no liquid, but the lining showed wrinkling at the first stages of the folding which would have led to the formation of a corpus luteum. At a slightly later stage as the folding of the follicular wall becomes more obvious the centre of the ruptured follicle is often filled with a translucent gel, presumably the tertiary liquor folliculi of Brambell (1930, p. 121). Such a stage is shown in Plate 4.

There is a very wide range of follicle diameter immediately after rupture, from 22 to 60 mm (median 37 mm) but it is doubtful whether these diameters can be compared directly with those of turgid follicles just prior to rupture. The smallest burst follicle, 22 mm in diameter, was possibly not normal as here two follicles (22 and 23 mm) had burst simultaneously. This was one of two cases of double ovulations recorded in the present study. Omitting this double ovulation, only four of the 35 females taken immediately after ovulation had burst follicles below 30 mm in diameter (26, 27, and 28 mm) and these when turgid prior to rupture would very probably have exceeded 30 mm in diameter, in agreement with the observation in part (*b*) above that maturing Graafian follicles were from 30 mm in diameter. Figure 3 shows that the upper limit of follicle diameter at ovulation is over the 60 mm maximum recorded for a burst follicle as one apparently normal mature follicle reached 105 mm in diameter. This follicle had a very thin, almost transparent area on the surface, indicating it was close to the point of rupture.

(*d*) *Graafian Follicle During Pregnancy*

Although several very small embryos have been found in east Australian coast female humpbacks, no records of early pregnancy are available as yet from females taken off the western coast, despite careful searching of the uteri of females whose ovaries contained a developing corpus luteum. Females in late pregnancy were not of infrequent occurrence. The diameters of the largest Graafian follicle in each set of ovaries from 45 of these are shown in Table 3.

TABLE 3

DIAMETER OF LARGEST GRAAFIAN FOLLICLE IN LATE PREGNANT FEMALES

Diameter Largest Follicle (mm)	No. of Late Pregnant Females	Diameter Largest Follicle (mm)	No. of Late Pregnant Females
2	2	10	2
3	5	11	2
4	3	12	—
5	9	13	—
6	10	14	—
7	4	15	1
8	4	16	—
9	2	17	—
		18	1

Table 3 shows that female humpback whales in late pregnancy have much reduced Graafian follicles (median value 6 mm), well below the range in resting mature females (median value 20 mm). In only two cases of late pregnancy were follicles approaching the size in resting females (diameters 15 and 18 mm respectively) and these, like all follicles in the ovaries of late pregnant females, appeared to have undergone a good deal of resorption. Generally follicles are so reduced that there is little more than a thickened wall with very little space for the liquor folliculi. These reduced follicles do not project from the wall of the ovary and are not at all obvious, as can be seen from Plate 6.

This marked reduction in follicle size at late pregnancy in the humpback whale is not in agreement with the results in blue and fin whales recorded by Mackintosh and Wheeler (1929) who stated that in those whales "There are invariably many enlarged follicles in the ovaries of pregnant whales and these range from 40 mm. to 50 mm. in diameter to 10 mm. and less". Also Nishiwaki and Oye (1948) recorded large follicles in pregnant blue and fin whales, and indicated that the largest Graafian follicles exceeded those of resting females. But both British and Japanese workers obtained their records from Antarctic waters, where most of the pregnant females would have been in earlier stages of pregnancy. It is possible that resorption of follicles would not have been evident until later stages. The large follicles in early pregnancy reported by both sets of workers had apparently matured just before the females' present pregnancies and had not yet atrophied. Indirect evidence of reduction in follicle size in late pregnancy in blue and fin whales is afforded by Mackintosh and Wheeler's observation that follicles were reduced during lactation.

(*e*) *Graafian Follicles During Lactation*

(i) *Early Lactation.*—Diameters of the follicles in the early stages of lactation are available from three females, the largest follicles being 6, 8, and 26 mm respectively. The first two are within the range of follicle size found in late pregnancy (see above) and are to be expected soon after parturition, while in the third this larger follicle was presumably an example of one follicle maturing just before the onset of a pregnancy resulting from a previous ovulation and while a good deal of resorption may have taken place, this follicle remained above normal size during pregnancy and in lactation up to the time the female was killed. Mackintosh and Wheeler (1929, p. 388) recorded that in blue and fin whales, "during lactation one or two large follicles are found but the smaller ones are no longer visible" (on the surface of the ovary).

(ii) *Mid Lactation.*—At this stage follicles have begun to increase in size, but the largest are still in the lower part of the range found in the ovaries of resting females, the largest follicles from three females in mid lactation being 11, 15, and 18 mm respectively.

(iii) *Late Lactation.*—Maximum follicular diameters are available from 60 normal cases of this stage, with a range of 10-50 mm, and in a few cases ovulation had very recently taken place, so that in some female humpback whales maturation of follicles or even ovulation takes place without a resting (anoestrus) phase following lactation.

These females in late lactation could be divided into two groups, those with no maturing follicles, and those with follicles maturing or recently burst; 82 per cent. were in the former group, having a maximum follicular diameter ranging from 10 to 28 mm with a median value of 20 mm, the same as that found in the ovaries of resting females, while 18 per cent. had maturing follicles (diameters 35-50 mm) or had recently ovulated.

One anomalous case of late lactation was recorded in which the female was pregnant. Here the largest follicle was reduced to 11 mm in diameter. This female (No. 54 of the Carnarvon station's 1952 catch) was carrying a 9 ft 3 in. foetus when killed in mid June. This was a rather small size for that month, but this might be expected in an unusual case of a further pregnancy beginning shortly after the previous parturition (see Section VI(*c*)).

(*f*) *Ovarian Cysts in Older Females*

Four Western Australian coast females were found to have large cysts attached to the ovaries. These females were relatively old, there being from 27 to 34 'corpora lutea' in the ovaries and full physical maturity had been reached in the three whose vertebral epiphyses were examined. It is thought that these cysts were degenerate Graafian follicles. Only one of four physically mature females examined had normal ovaries with no cysts attached and these showed a total of 38 'corpora lutea'.

Data concerning the four cases where ovarian cysts were present are summarized as follows:

No. 163 from Carnarvon, 1951:

Total length 45.5 ft; 34 'corpora lutea', one recently developed. Several thin-walled liquid-filled cysts hanging away from both ovaries. Largest cyst on one ovary 72 mm in diameter while largest on the second ovary was 100 mm. The liquid from the larger cysts on the second ovary weighed 1140 g. It was difficult to decide which were smaller cysts and which were normal Graafian follicles. A fully physically mature female.

No. 599 from Carnarvon, 1951:

Total length 43.0 ft; 29 'corpora lutea', one very recently developed. Several thin-walled cysts (filled with clear liquid) to 65 mm in diameter hanging from the ovaries. Fully physically mature.

No. 313 from Point Cloates, 1952:

Total length 45.2 ft; 27 'corpora lutea'; none recent. Large thin-walled cysts to 150 mm in diameter containing clear liquid. Graafian follicles 15-20 mm in diameter were thick-walled and possibly non-functional. A fully physically mature female.

No. 363 from Point Cloates, 1952:

Total length 43.5 ft; 29 'corpora lutea'; none recent. This female had just ovulated. Several thin-walled cysts 36-71 mm in diameter. Vertebral epiphyses not examined.

V. CORPORA LUTEA

(*a*) *Early Development After Ovulation*

Growth and folding of the follicular epithelium with the formation of luteal tissue begins very soon after ovulation so that the vesicle remaining after rupture of the Graafian follicle is soon filled with luteal tissue, although some translucent gel sometimes occupies the centre of the newly formed corpus luteum. Plate 4 shows an early stage in this process. A recently developed corpus luteum can readily be distinguished from later stages, the outer membrane being very thin with numerous blood vessels visible immediately beneath it. The luteal tissue is soft, pale, and expanded in contrast to the firmer yellow tissue in late pregnancy and early lactation. Plate 5 shows a section through a recently developed corpus luteum.

The initial size of a corpus luteum after formation is dependent upon the size of the follicle at ovulation. It was shown above that maturing follicles reach 30 mm in diameter before rupture. This is in agreement with measurements of early corpora lutea, the smallest having a diameter of 32 mm. But once formed, the corpus luteum continues to develop, increasing in size. Figure 4 shows the maximum diameter of the recently formed corpora lutea from Western Australian coast female humpbacks and the date upon which these females were killed. It is seen that larger glands are found later in the season. The broken line in Figure 4 linking the largest corpora lutea found in each month indicates a probable growth curve of those corpora lutea developed from ovulations earlier in the season. During the first 2 months of development the corpus luteum steadily increases in size, the growth then slowing down as the maximum diameter approaches the range found in corpora lutea of late pregnancy.

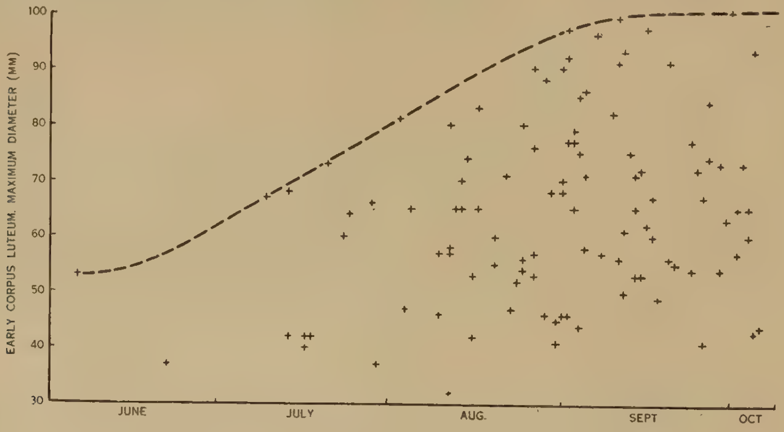

Fig. 4.—Maximum diameter of early corpora lutea.

The small recently formed corpora lutea found late in the catching season (late September and early October, see Fig. 4) indicate that ovulation continues throughout the winter and early spring.

In each case of an early corpus luteum shown in Figure 4 the uterus of the female was carefully searched for an early embryo but none was found. However, if pregnancy had begun the embryo would have been very small, and in the short time available for examination of the uterus it could easily have been missed. Because of this failure to establish whether or not pregnancy had begun in the individuals represented in

Figure 4, it is not known how far development of a corpus luteum proceeds if ovulation is not followed by pregnancy.

(*b*) *Corpora Lutea of Pregnancy* (*Corpora Graviditata*)

All pregnant females from the Western Australian coast so far examined were in late pregnancy (foetuses from 9 ft 3 in. to 17 ft 6 in.).

TABLE 4

FEMALES IN LATE PREGNANCY: OVARY AND FOETUS RECORDS

Functional Corpus Luteum			Ovary Weights (g)		Total Corpora Lutea	Foetus	
Weight (g)	Dimensions (mm)	Mean Dia. (mm)				Sex	Length
305	106 × 79 × 74	86	—	—	2	♀	3.81
327	96 × 93 × 74	88	—	—	4	♂	3.93
422	102 × 97 × 78	92	—	—	38	♂	4.30
450	107 × 86 × 85	93	940	343	7	♂	3.90
633	121 × 113 × 81	105	—	—	2	♂	4.36
643	144 × 120 × 67	110	—	—	30	♂	4.27
657	116 × 100 × 95	104	—	—	6	♂	3.60
770	132 × 117 × 100	116	—	—	10	♂	4.54
822	136 × 134 × 87	119	—	—	16	♀	5.06
860	130 × 110 × 92	111	1765	530	10	♀	4.30
860	137 × 123 × 95	118	—	—	3	♀	3.78
867	147 × 121 × 97	122	—	—	9	♂	4.02
873	150 × 103 × 96	119	—	—	7	♂	5.27
876	124 × 111 × 110	115	—	—	5	♀	4.91
970	145 × 125 × 91	120	1890	640	17	♀	4.15
1005	145 × 117 × 107	123	1755	760	14	♀	2.83
1082	135 × 130 × 105	123	—	—	22	♀	5.03
1194	162 × 152 × 88	134	—	—	15	♀	4.54
1215	140 × 138 × 106	128	—	—	8	♂	4.63
1231	140 × 127 × 100	122	—	—	8	♀	5.24
1395	170 × 136 × 118	141	—	—	24	♀	3.60
1412	173 × 157 × 95	142	—	—	14	♂	4.33
1449	163 × 126 × 123	137	—	—	18	♂	5.33
1475	160 × 135 × 130	142	—	—	11	♀	4.48
1597	185 × 165 × 85	145	—	—	25	♀	4.36
1695	165 × 158 × 117	147	—	—	7	♂	4.54
1711	155 × 145 × 130	143	—	—	21	♂	3.90
1945	196 × 162 × 125	164	—	—	7	♀	4.66
2185	205 × 160 × 100	155	3204	632	7	♂	4.27
Median of mean dimensions of corpora lutea		122					
Mean of mean dimensions of corpora lutea		123					

The functional corpora lutea of these females showed great variability in weight and size, ranging from 305 g (106 by 79 by 74 mm) to 2185 g (205 by 160 by 100 mm). Details of the cases of late pregnancy where the functional corpus luteum was weighed are shown in Table 4. The three measurements of a corpus luteum were obtained by first taking the greatest diameter and then the lengths of the two axes at right angles to this.

The weight of the corpus luteum in late pregnancy is not a function of total ovary weight. Functional corpora lutea weights were from 35 to 57 per cent. of the total ovary weight.

The sex of the near-term foetus was found to have no bearing on this wide variation in functional corpora lutea weight. In 15 cases of late pregnancy where the foetus was a male the functional corpus luteum ranged from 327 to 2185 g, with a mean weight of 1021 g, while in 14 cases with a female foetus the corresponding range was 305-1945 g, mean **1116** g.

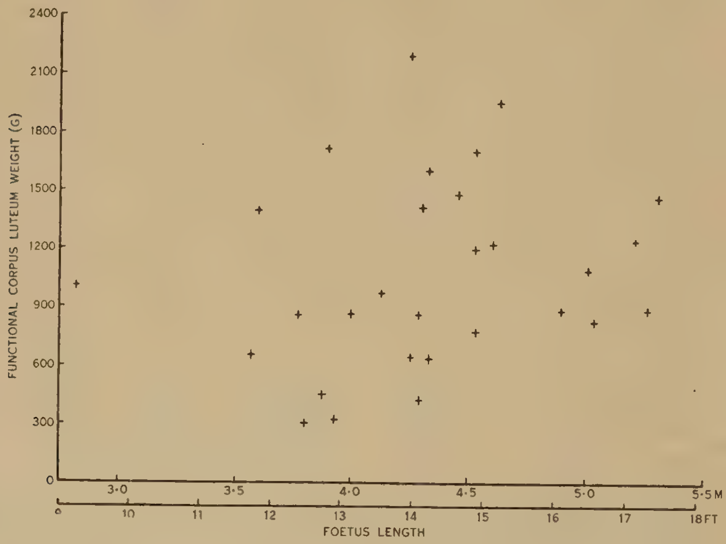

Fig. 5.—Weight of functional corpus luteum and foetal length.

Mackintosh and Wheeler (1929, p. 388) stated that there was some indication in fin and blue whales that the corpus luteum of pregnancy increased in size up to the stage when the foetus measured 1 m, and thereafter decreased, probably up to the end of gestation. In Section V (*a*) an early increase in corpus luteum size was shown (Fig. 4) but the state of pregnancy was not established. In Figure 5 the weight of the functional corpus luteum is shown against length of foetus, using the records from Table 4. This scatter diagram does not indicate any relationship between functional corpus luteum weight and the stage of gestation (the latter based on foetal length).

Table 5 shows data from female humpbacks in early pregnancy extracted from Matthews's (1937) report. The range of the functional corpora lutea weights in early pregnancy from these South Georgian specimens was only slightly below that shown in Table 4 for Western Australian coast females in late pregnancy.

In Figure 6 the mean diameters of the functional corpora lutea have been plotted against foetal length, including the data from Tables 4 and 5. This figure shows little variation of size of functional corpora lutea with the stage of gestation, unless perhaps a slight increase in functional corpus luteum size in advanced pregnancy. Thus the evidence from corpora lutea weights and measurements does not agree with the decrease in size of the functional corpus luteum as pregnancy advances suggested by Mackintosh and Wheeler for blue and fin whales.

TABLE 5

FEMALES IN EARLY PREGNANCY; SOUTH GEORGIA (FROM MATTHEWS 1937)

	Functional Corpus Luteum		Ovary Weights (g)		
	Mean Diameter (mm)	Weight (g)	Ovary Carrying Corpus Luteum	Inactive Ovary	Foetus Length (cm)
	66	—	—	—	68
	78	270	790	—	28
	95	—	1814	—	38
	100	400	740	340	76
	110	—	—	—	75
	130	1050	1640	680	70
	140	—	—	—	51
	160	1810	2680	620	4
Mean	110				

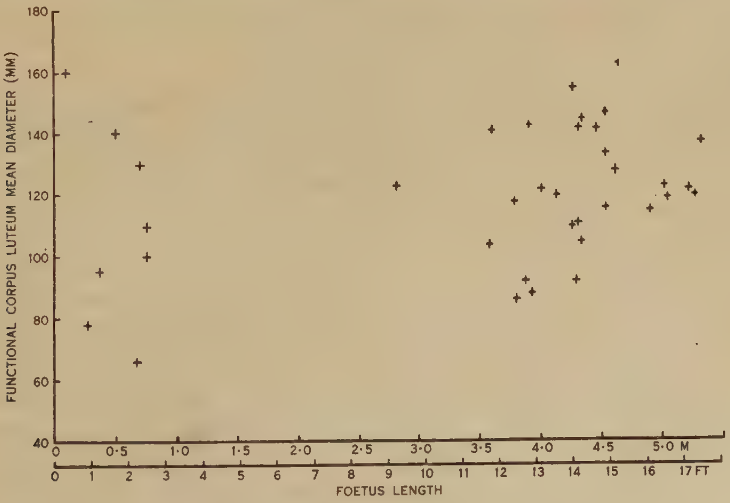

Fig. 6.—Mean diameter of functional corpus luteum and foetal length.

On the available evidence there would appear to be some relationship between the weight of the functional corpus luteum and the age of the late pregnant female, using the total number of corpora lutea as an index of relative age. In Figure 7 the weight of the functional corpus luteum is shown against the total corpora lutea in the ovaries of 29 females in late pregnancy. The weight of the functional corpus luteum in these tends to increase with increasing numbers of corpora lutea but is again low in relatively old females (having 30 and 38 'corpora lutea' in the ovaries).

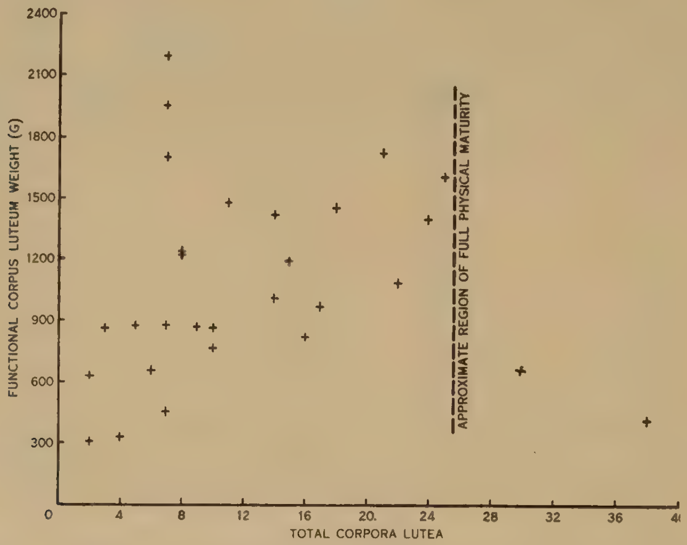

Fig. 7.—Females in late pregnancy: functional corpus luteum weight and total corpora lutea.

In one pregnant female two corpora lutea had all the characteristics of normal functional corpora lutea, though both were smaller than usual. This female was carrying a male foetus 3.96 m (13.0 ft) long. In one ovary the functional corpus luteum measured 98 by 94 by 54 mm, while in the other ovary the functional corpus luteum measured 76 by 75 by 57 mm. Respective ovary weights were 780 and 765 g, unusually close together for a case of late pregnancy as seen from ovary weights in Tables 4 and 5. In this case probably two Graafian follicles had burst simultaneously, one ovum having failed to be fertilized, or the zygote being lost, but both follicles developing into functional corpora lutea, neither of which reached the size range of single functional corpora lutea in late pregnancy. Such a condition must be regarded as rare in the humpback whale.

(*c*) *Resorption of the Corpus Luteum During Lactation*

After parturition the resorption of the functional corpus luteum (corpus graviditatum) is very rapid. Table 6 shows the range and mean size of the corpora lutea in stages from the active state (in late pregnancy) until late in lactation.

In early lactation the resorption of the corpus graviditatum has already begun, as indicated by a decrease in size. But the gland still hangs away from the main portion of the ovary and has a tight, relatively thin outer membrane with many blood vessels below this. The luteal tissue still has the wide expanded convolutions as seen during late pregnancy. By mid lactation the resorption of the corpus luteum is well advanced (Table 6). Blood vessels are still visible in the enclosing capsule which is now thickening with fibrous tissue. By the last few weeks of lactation the resorption of the corpus luteum has proceeded so far that it seldom shows any signs of its earlier activity and must now be classed as a corpus albicans. The resorbed luteal tissue is now enveloped in a thick fibrous capsule and does not usually project far from the ovarian surface. In fact it is often difficult in late lactation to determine which of the corpora albicantia had been most recently functional so that for the measurements used for late lactation in Table 6

TABLE 6
RESORPTION OF FUNCTIONAL CORPORAL LUTEA

	Average Diameter (mm)
(i) Corpora lutea in late pregnancy	
Largest 196 × 162 × 125 mm	164
Smallest 106 × 79 × 74 mm	86
Mean of average diameters from 29 corpora lutea of late pregnancy	123
(ii) Corpora lutea in early lactation	
Dimensions (mm) 140 × 110 × 90	113
111 × 97 × 75	94
95 × 70	83
Mean of average diameters of 3 corpora lutea of early lactation	97
(iii) Corpora lutea in mid lactation	
Dimensions (mm) 92 × 84 × 80	85
97 × 73 × 68	80
102 × 78 × 58	79
91 × 72 × 67	77
89 × 81 × 61	77
83 × 64	74
Mean of average diameters of 6 corpora lutea of mid lactation	79
(iv) Corpora lutea in late lactation (now corpora albicantia)	
Largest 86 × 76 × 63 mm	75
Smallest 40 × 27 mm	33
Mean of average diameter of 62 corpora lutea of late lactation	50

the largest corpus albicans has been taken as the remnant of the most recently functional corpus luteum.

From this stage, further resorption of the corpus albicans is very slow and although some may be reduced to a mean diameter of 6 mm there is little doubt, as shown by Mackintosh (1942, p. 220), that in whales the corpora albicantia persist, if not throughout life, then at least until long after physical maturity has been reached.

VI. Time and Frequency of Ovulation

(*a*) *Time of Ovulation*

Table 7 summarizes the variations in the condition of the ovaries as found in 290 mature Western Australian coast females, excluding females in late pregnancy and early lactation. Those in late lactation have been included in the respective column indicated by the state of the ovaries.

Table 7

STATE OF THE OVARIES OF MATURE FEMALES IN 10-DAY PERIODS, EXCLUDING FEMALES IN LATE PREGNANCY AND EARLY LACTATION

Ten-day period	Total No.	Resting Ovaries		Maturing Follicle		Burst Follicle		Early Corpus Luteum	
		No.	%	No.	%	No.	%	No.	%
June 1-10	22	20	90.0	1	4.5	0	—	1	4.5
June 11-20	25	25	94.0	2	8.0	0	—	0	—
June 21-30	24	15	62.5	8	33.3	0	—	1	4.2
July 1-10	18	6	33.3	9	50.0	2	11.1	1	5.6
July 11-20	35	4	11.4	22	62.9	6	17.1	6	17.1
July 21-30	17	2	11.8	6	35.3	8	47.1	4	23.5
July 31-Aug. 9	13	1	7.7	8	61.5	3	23.1	5	38.5
Aug. 10-19	24	3	12.5	7	29.2	4	16.7	14	58.3
Aug. 20-29	25	5	20.0	7	28.0	5	20.0	13	52.0
Aug. 30-Sept. 8	29	3	10.3	9	31.0	2	6.9	21	72.4
Sept. 9-18	25	0	—	6	24.0	4	16.0	19	76.0
Sept. 19-28	20	4	20.0	4	20.0	0	—	13	65.0
Sept. 29-Oct. 8	13	1	7.7	4	30.8	0	—	11	84.6

The above percentages are graphed in Figure 8 to indicate the sequence of events from June to early October in the ovaries of mature females which were not in advanced pregnancy nor had recently given birth to a calf. Figure 8 shows that, off the Western Australian coast for the greater part of June, almost all (over 90 per cent.) of the above described class of mature females have ovaries in the resting condition, though in a small percentage of cases a maturing follicle or an early corpus luteum is present. Over 70 per cent. of these mature females with ovaries in the resting state taken in early June were in late stages of lactation. At the end of June, as the proportion of females with resting ovaries began to decrease, so the numbers of females in late lactation began falling, while the proportion of females with a maturing Graafian follicle in the ovaries increased.

By mid July only a small part of this group of mature females had resting ovaries, and numbers in this group remained relatively low for the rest of the winter and spring. But in mid July the proportion of females having a mature follicle in the ovaries reached a maximum, followed by a drop in the latter part of July when the frequency of occurrence of ruptured follicles reached its maximum. A secondary increase of females with a mature follicle early in August was not followed by a rise in ovulation frequency. This may be due to a movement of part of the population at this time. It has been shown (Chittleborough 1953) that increasing numbers of humpbacks turn southwards during August, while many are still travelling up the coast. However, while females with a mature follicle were less frequent from mid August to October, Figure 8 indicates that maturation of follicles and ovulation continue on a lessened scale until at least early October.

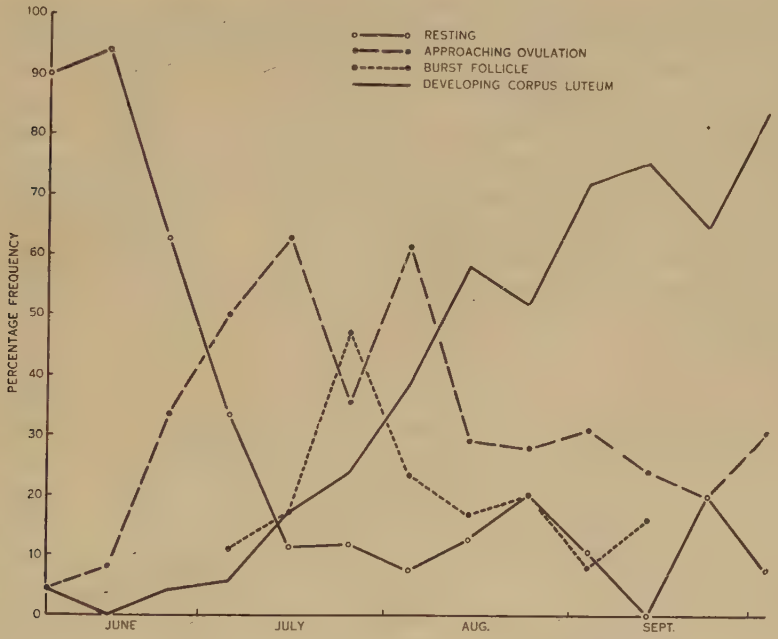

Fig. 8.—State of ovaries in mature females excluding late pregnant and early lactating females.

The maximum frequency of occurrence of ruptured follicles in the latter half of July was at a lower level than other stages (Fig. 8) owing to the fact that the transformation of a mature Graafian follicle to an early corpus luteum is a relatively fast process so that fewer females are killed in just this phase.

The proportion of females with a developing or recently developed corpus luteum, initially very low in June, increased in July and after the July maxima of maturing and burst follicles, became higher from August to October, by which time over 80 per cent. of the mature females not in late pregnancy or early lactation had at least one early corpus luteum in the ovaries.

From the above it would appear that off the Western Australian coast in June the mature female humpback whales (excluding those in late pregnancy and early lactation) are generally in late lactation, sometimes having ceased lactating, but with ovaries in the resting condition. In late June and early July, as lactation terminates (and sometimes before, as discussed below), maturation of at least one Graafian follicle usually begins. This is followed by ovulation generally in the latter half of July. But after this period of maximum frequency of ovulations, ovulation continues to occur with lesser frequency up to at least early October. The presence of an occasional female with an early corpus luteum in early June shows that ovulation does occur in a few females in late May or early June.

Since by the end of the catching season over 80 per cent. of the mature females which were not about to give birth, or had just given birth to a calf, had ovulated during the catching season (as judged by the presence of an early corpus luteum), a 2-yr breeding cycle can be inferred for the majority of female humpbacks, i.e. pregnancy occupying most of the first year (as given by Matthews), lactation extending over the greater part of the second year, with ovulation occurring at the end of the second year. On present evidence it appears that lactation occupies a greater period (a total of approx. 10 months) than that indicated by Matthews (1937) for female humpbacks in the South Atlantic Ocean.

(*b*) *Frequency of Ovulation During the Ovulatory Period*

As shown by Figure 8, ovulation first occurs early in June and continues throughout the Australian catching season, possibly into November, though no records are available for this month. June to November has been taken as the ovulatory period. Table 8 has been drawn up to indicate ovulation frequency in 10-day periods from June to October, using only mature females which were approaching ovulation or had ovulated once or more during the season in which they were killed. From this table the curves in Figure 9 have been drawn to show the trends in the ovaries of ovulating females as the catching season progressed. The frequency of occurrence of ovaries with one maturing follicle (curve *F*) decreased from June to July as the frequency of occurrence of ovaries bearing the first corpus luteum rose (curve *C*). These two curves cross in the latter half of July, in close agreement with the time of maximum ovulations shown in Figure 8.

For analysis of the frequency of ovulation during the catching season off the Western Australian coast, the positions of the curves of Figure 9 at the end of the season must be compared. By early October, Figure 9 shows that 62 per cent. of the ovulating females had ovulated once with no further follicles maturing (curve *C*). In a further 10 per cent. (curve *F*) the first maturing follicle of the season was present. It is possible that most of these females with a maturing follicle would have ovulated once before returning to the southern summer feeding grounds, so that a total of 72 per cent. of the ovulating females could have ovulated no more than once during the ovulatory period (June to November).

TABLE 8

WESTERN AUSTRALIAN COAST FEMALES OVULATING OR APPROACHING OVULATION: OVULATION FREQUENCY FROM JUNE TO OCTOBER

10-Day Period	Total Ovulating (or about to ovulate)	Approaching First Ovulation of Season		Ovulated Once: No Further Follicles Maturing		Ovulated Once: Second Follicle Maturing		Ovulated Twice: No Further Follicles Maturing		Ovulated Twice: Third Follicle Maturing	
		No.	%	No.	%	No.	%	No.	%	No.	%
June 1-10	2	1*	50	1*	50	—	—	—	—	—	—
June 11-20	2	2	100	—	—	—	—	—	—	—	—
June 21-30	9	8	89	1	11	—	—	—	—	—	—
July 1-10	12	9	75	3	25	—	—	—	—	—	—
July 11-20	31	19	61	9	29	3	10	—	—	—	—
July 21-30	15	4	27	8	53	2	13	1	7	—	—
July 31-Aug. 9	12	4	33	4	34	4	33	—	—	—	—
Aug. 10-19	21	2	10	14	66	5	24	—	—	—	—
Aug. 20-29	20	2	10	12	60	5	25	1	5	—	—
Aug. 30-Sept. 8	26	3	12	17	65	6	23	—	—	—	—
Sept. 9-18	25	2	8	16	64	4	16	3	12	—	—
Sept. 19-28	15	3	20	10	66	1	7	1	7	—	—
Sept. 29-Oct. 8	12	1	8	7	58	2	17	1	8	1	8

* Numbers within this period too small to be significant.

In early October 12 per cent. of the ovulating females had ovulated once and had a second follicle maturing. If these females had conceived at the first ovulation, this second maturing follicle would atrophy, but if conception had not taken place it would probably have burst before these females returned to the Antarctic feeding grounds. Only 8 per cent. of the ovulating females had ovulated twice during the season by early October, and showed no sign of further maturing follicles (curve *CC*).

A further 8 per cent. had ovulated twice by early October and had a third follicle maturing (curve *CCF*), so that three ovulations in one season could have occurred in this group if conception had not already taken place.

The situation amongst ovulating females by the beginning of October was that a minimum of 62 per cent. (from curve *C*) had ovulated once only, with a possible maximum of 84 per cent. (from curves $C + F + CF$) which may not have ovulated more than once during the season. A minimum of 16 per cent. (curves $CC + CCF$) had ovulated twice during the season with a possible maximum of 28 per cent. (curves $CC + CCF + CF$), while from 0 to 8 per cent. might have ovulated three times during the ovulatory period.

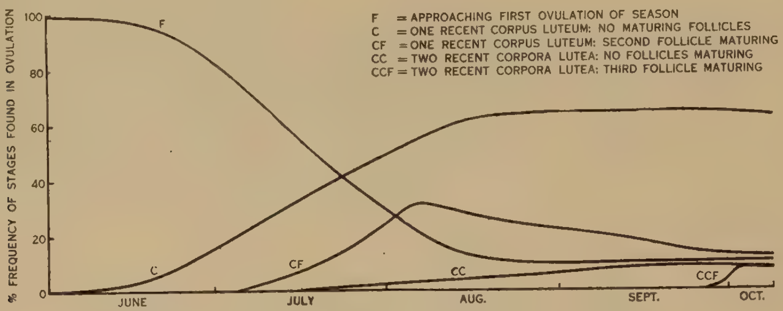

Fig. 9.—Ovulating females only: stages in ovulation.

Thus between June and October the proportions of ovulating females which ovulated once, twice, and three times respectively were variable, mainly because, of the cases where ovulation had already occurred, another follicle was maturing, but the fate of the previously discharged ovum was unknown. However, it can be said that the greatest proportion of the female humpbacks during their ovulatory period ovulated only once, few ovulating twice, and on present evidence, rarely three times.

From the present evidence it appears that the mean number of ovulations per female humpback during the ovulatory period was only slightly above 1, less than the 1.9 for blue, and 1.8 for fin whales as estimated by Dr. N. Peters (see Mackintosh 1942, p. 227). Matthews's estimate of five ovulations for each sexual cycle of 2 yr in female humpbacks appears to have been far too high.

The analyses above are based upon the assumption of a 2-yr breeding cycle in female humpbacks. As indicated earlier, most of those mature females not in late pregnancy or lactating do ovulate between June and November, but as shown in Figure 8, a small part (a little over 10 per cent.) of these females show no sign of ovulating during the general ovulatory period. In these one of two possibilities might apply. It may be that occasionally mature female humpback whales undergo a lengthened period of anoestrus so that instead of a normal 2-yr sexual cycle, the cycle extends over 3 yr. The second possibility is that these females with ovaries resting throughout the period when ovulation should normally have taken place might be out of phase and could ovulate during the summer while feeding in southern waters. This latter explanation is the most likely, as Matthews recorded one humpback foetus from South Georgia 0.31 m (12¼ in.) long in May when foetuses were generally about 2.7 m (8 ft 10 in.) long. Also at the Point Cloates (W.A.) station a foetus 1.45 m (4 ft 9 in.) long has been recorded in July, when foetuses were generally in the region of 4.2 m (13 ft 9 in.). In both of these cases, conception must have taken place in December or January. Mackintosh and Wheeler indicate that in blue and fin whales ovulation (and possibly conception) may occasionally take place during the southern summer.

(*c*) *Ovulation During Lactation*

As indicated in Section VI (*a*), over 70 per cent. of the mature females with ovaries in the resting state taken in early June were in late stages of lactation. Generally lactation terminated before Graafian follicles began maturing, but occasionally during the last stages of lactation (June or early July) a mature follicle was found in the ovaries, and sometimes, generally when lactation appeared to have been continued somewhat later than usual, ovulation had even taken place and an early corpus luteum was present in the ovaries.

Since present evidence strongly suggests that lactation in female humpbacks extends longer than the 5 months indicated by Matthews, generally continuing until the first part of the succeeding ovulatory period, it might be expected that occasionally a follicle matures or even ovulation takes place, shortly before the termination of lactation.

One case has been found amongst Western Australian coast females where ovulation had very recently occurred in a female in a fairly early stage of lactation. This was whale No. 196 of the Carnarvon station's 1951 catch, killed on August 2. A recently functional corpus luteum measuring 102 by 78 by 58 mm was found in one ovary, while one Graafian follicle 34 mm in diameter had recently burst and a second follicle 36 mm in diameter was maturing. As Matthews indicated, ovulation during early lactation could give rise to two pregnancies in 3 yr, but this must be regarded as abnormal in female humpback whales.

Further evidence for two pregnancies occasionally occurring in 3 yr was obtained from whale No. 54 of the Carnarvon station's 1952 catch. This female, killed on June 15, was carrying a foetus 9 ft 3 in. long, yet was lactating copiously. This case must have been similar to that of No. 196 discussed above: ovulation (followed by pregnancy in this instance) taking place shortly after parturition, so that by the following June this female was in relatively advanced pregnancy yet still lactating in association with the previous pregnancy.

(*d*) *Multiple Ovulations*

From over 330 mature female humpback whales examined in detail on the Western Australian coast, two examples of multiple ovulations have been found. One of these has already been described in Section V(*b*). In this, two follicles had apparently burst simultaneously, one from each ovary, only one ovum being successfully fertilized, so that when this female was killed in late pregnancy two functional corpora lutea were present but only one foetus. Similar occasional examples of females with more than one functional corpus luteum have been recorded by Wheeler (1930) in fin whales. The second has been mentioned in Section IV(*c*). This female (No. 448 of the Point Cloates station's 1952 catch), 38 ft 5 in. long, having one corpus albicans in the ovaries, had two very recently burst Graafian follicles, the collapsed diameters of which were 23 and 22 mm respectively. As pointed out in Section IV(*c*), these were much below the normal diameters of burst follicles.

During the ovulatory period, especially in June and July, it was not uncommon to find that two or more Graafian follicles (six in one whale) were maturing in one set of ovaries. But these cannot be regarded as potential multiple ovulations as in such a pair of ovaries there was a gradation in follicle diameter; for example, where the six maturing follicles were present the respective follicle diameters were 53, 37, 35, 34, and 30 mm. The largest follicle would probably have burst first, followed by succeeding ones if conception failed to take place.

The presence of more than one ovum in a Graafian follicle represents another possible type of multiple ovulation. A potential example of this occurring in humpback whales was found in a late foetal ovary, where one early Graafian follicle contained three ova, as shown in Plate 2.

From the present evidence, multiple ovulations in female humpback whales must be regarded as rare.

VII. DISCUSSION

An increase in paired ovary weight with increasing body length has been shown for female humpback whales, but owing to the wide range of ovary weights found just prior to and after sexual maturity (Fig. 1) there is no sharp distinction between immature and mature females on a basis of ovary weight.

Little evidence has been found of a continued increase in ovary weight with increasing age after the attainment of sexual maturity (Fig. 2), or of a decrease in ovary weight in older female humpback whales, noted by Mackintosh and Wheeler (1929) in fin and blue whales and assumed by Matthews (1937) to take place in humpback whales.

From the available material it has been found that in female humpback whales Graafian follicles up to a size of 0.13 mm in diameter are present just prior to birth. Follicles initially develop in the early years of life until from 11 to 29 mm in diameter, with a median value of 20 mm. These are the advanced but resting follicles, one (or more) of which enlarges and matures during the ovulatory period. Such resting follicles may be found in immature females close to or within the maturing length range, as well as in mature females not pregnant or lactating (see Fig. 3).

At the approach of an ovulation, one of the resting follicles enlarges to exceed 30 mm in diameter (one, apparently normal, reached 105 mm) before rupture (Fig. 3). The median diameter of very recently ruptured follicles was 37 mm, with a range of 22-60 mm, but when turgid just prior to rupture such Graafian follicles would have had greater diameters.

After ovulation the ruptured follicle rapidly develops into a corpus luteum, sometimes enclosing a translucent gel, presumably the remnants of tertiary liquor folliculi (see Brambell 1930), in the centre. A relatively rapid increase in size of the early corpus luteum over the first 2 months is indicated, growth then slowing down as the corpus luteum approaches the size range of corpora lutea of late pregnancy. Since the presence or absence of an early embryo has not been definitely established in these cases of an early corpus luteum, it is not known how far development of a corpus luteum proceeds if ovulation is not succeeded by pregnancy.

The corpus luteum (or graviditatum) initially formed early in a pregnancy remains functional throughout the gestation period. Perry (1953) recorded that in the African elephant there are accessory corpora lutea developed during the gestation period, but this does not occur in the humpback whale. There is no evidence that the corpus graviditatum in the humpback whale decreases in size toward the end of pregnancy as was suggested by Mackintosh and Wheeler (1929) in fin and blue whales. Present evidence suggests that the corpus graviditatum, after an initial rapid increase in size, continues growing (though at a much reduced rate) until pregnancy is terminated. The weights of corpora graviditata shortly before parturition (305-2185 g) cannot be related to the length of the females, the total ovarian weight, or the sex or length of the foetus, but there appears to be some relationship between the weight of the corpus graviditatum just before parturition and the relative age of the female. Figure 7 indicates that the weight of the corpus graviditatum shortly before parturition tends to be lower in younger females, rising with increasing numbers of corpora lutea in the ovaries, but is again low in relatively old females (having 30 and 38 'corpora lutea').

After parturition the resorption of the corpus graviditatum is very rapid so that by the latter part of lactation it shows no sign of its earlier activity and must be classed as a corpus albicans.

During pregnancy the Graafian follicles remaining in the ovaries diminish greatly in size, the range of largest follicles found towards the end of pregnancy being 2-18 mm in diameter, with a median value of 6 mm (Table 3). After parturition the Graafian follicles in the adult ovaries soon begin increasing in size, so that by the latter part of lactation (which on present evidence extends over approx. 10 months) the diameters of the larger follicles are again within the resting range (11-29 mm) with a median diameter of 20 mm. In a minority of cases maturation of a follicle, and even ovulation, takes place a little before the termination of lactation.

On the available evidence the ovarian cycle in mature female humpback whales (excluding those in late pregnancy or early lactation) off the Western Australian coast between June and October may be summarized as follows:

In the greater part of June, most (over 90 per cent.) of the above class of females have ovaries in the resting condition, but over 70 per cent. of these females are in late stages of lactation. In late June and early July as lactation is terminated (occasionally before), maturation of a Graafian follicle begins in the majority of these females. While mature follicles are occasionally found in June, most are found in mid July, followed by maximum numbers of ovulations in the latter half of July (Fig. 8), after which ovulation is still of common occurrence until at least early October, probably extending into November. As shown in Figure 8, most mature females not in late pregnancy or early lactation ovulate during the ovulatory period (taken as June to November), since by early October less than 15 per cent. of these females had not ovulated and showed no signs of maturing follicles.

During the normal ovulation period (between June and November) the present study shows that most (62-84 per cent.) of the ovulating females do not ovulate more than once, some twice only (16-28 per cent.) and few (up to 8 per cent.) could have ovulated three times. These proportions indicate that the mean number of ovulations for a female humpback whale during its ovulatory period is only slightly over one, probably less than 1.5.

The probability that females occasionally ovulate (with conception succeeding) at other times of the year (for example, December or January) is indicated in Section VI(*c*).

From the material examined and the conclusion that almost all mature females not in late pregnancy or early lactation ovulate between June and November, a 2-yr breeding cycle in female humpback whales can be inferred; i.e. pregnancy occupying most of the first year, lactation extending over the greater part of the second year, with ovulation following shortly after the termination of lactation, at the end of the second year.

VIII. ACKNOWLEDGMENTS

Assistance given by whaling inspectors of the Western Australian Fisheries Department and the Commonwealth Fisheries Office in the collection of material and data at Western Australian whaling stations is gratefully acknowledged. Acknowledgment is also due to the management of the Norwest Whaling Company and the Australian Whaling Commission, for the use of facilities at their respective whaling stations. Mr. N. S. Stenhouse, Section of Biometrics, C.S.I.R.O., gave assistance with the analysis of results. Mr. G. W. Rayner, Division of Fisheries, C.S.I.R.O., read the manuscript, giving helpful advice. I am grateful to the University of Western Australia for laboratory facilities and to Professor H. Waring, Zoology Department, University of Western Australia, and Mr. K. Sheard, Division of Fisheries, C.S.I.R.O., for reading the manuscript.

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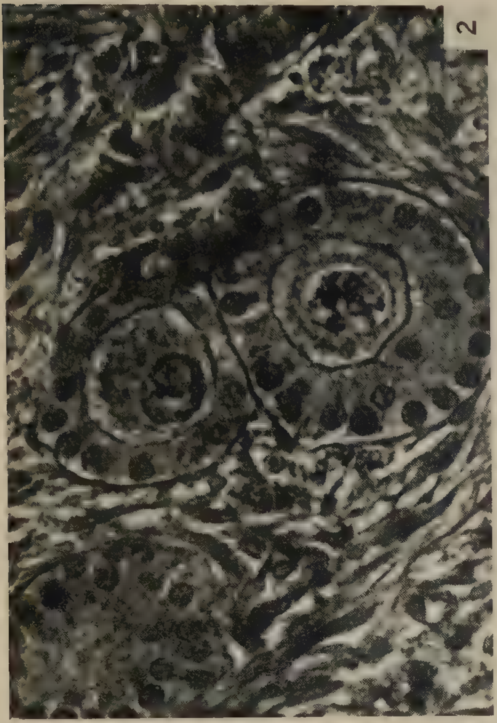
APPENDIX I

TOTAL LENGTH AND TOTAL OVARIAN WEIGHT

Immature Females		Resting Mature Females			
Total Length (ft)	Ovary Weight (g)	Total Length (ft)	Ovary Weight (g)	Total Length (ft)	Ovary Weight (g)
29.25	580	36.50	1045	41.83	2225
30.25	131	38.00	1480	41.92	3100
32.75	180	38.42	2230	42.08	1625
32.92	140	38.50	785	42.25	1556
33.50	208	38.75	550	42.42	1667
34.00	230	38.83	2167	42.58	965
34.33	512	39.00	1025	42·67	1105
34.58	270	39.08	720	42.67	3980
35·00	315	39.17	570	42.83	884
35.00	335	39.42	605	42.83	1185
35.08	795	39.42	1450	43.08	2129
35.08	1081	39.67	794	43.17	1050
35.17	550	39.75	650	43.17	1155
35.58	623	39.75	832	43.17	1780
35.75	640	39.92	2112	43.25	1042
36.08	511	39.92	2845	43.33	1860
36.17	255	40.00	778	43.42	3730
36.17	3425	40.08	1303	43.58	860
36.83	660	40.17	1017	43.58	1367
37.00	462	40.17	1310	43·75	1870
37.08	310	40.33	968	43.83	1845
38.00	960	40.58	2605	43.92	920
39.00	835	40.83	621	44.00	810
39.42	720	40.83	625	44.00	1470
40.50	665	40.92	907	44.25	1162
40.67	988	41.00	850	44.25	1301
40·83	1520	41.17	1466	45.00	1530
41.00	2045	41.17	1805	45.33	1825
		41.17	1969	45.42	1770
		41.17	2035	45.50	2160
		41.17	2840	45.75	1795
		41.33	3621	46.00	1310
		41.42	886	46.00	2675
		41.42	994	46.50	1776
		41.50	2305	46.50	3004
		41.58	1015	47.75	2045
		41.75	2780	49·25	2180
		41.83	1450		

OVARIES OF HUMPBACK WHALE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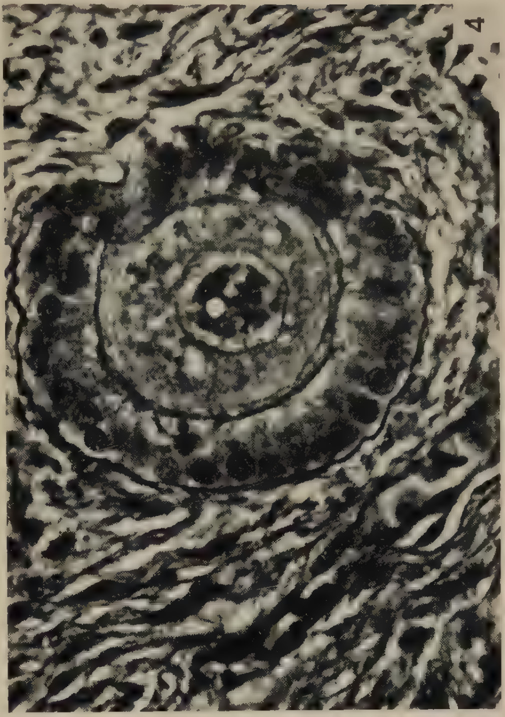
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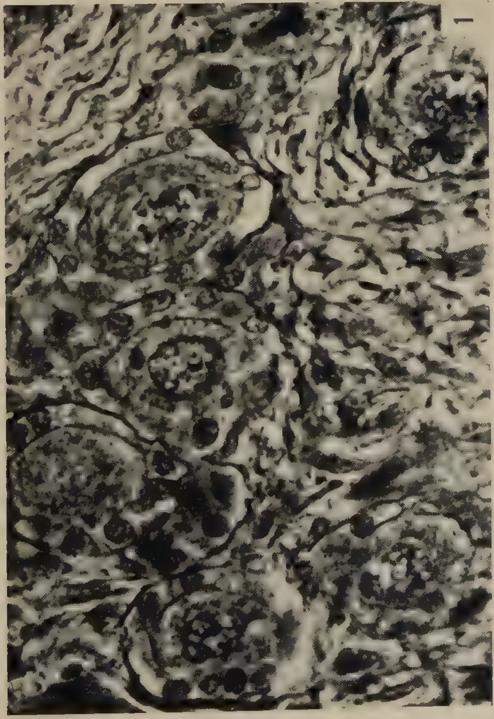
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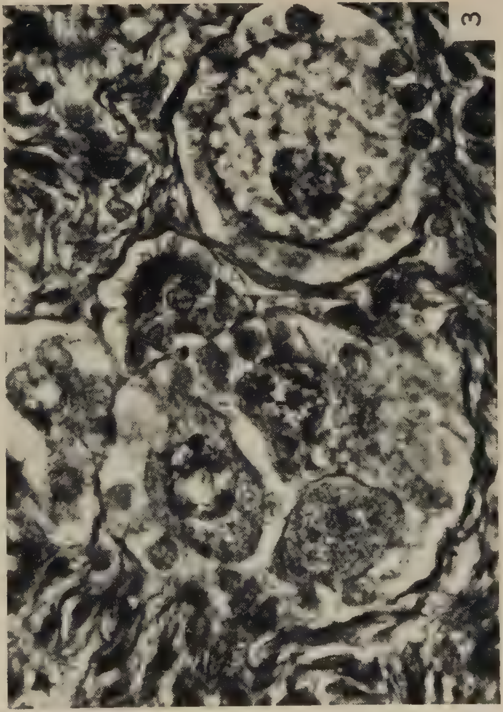
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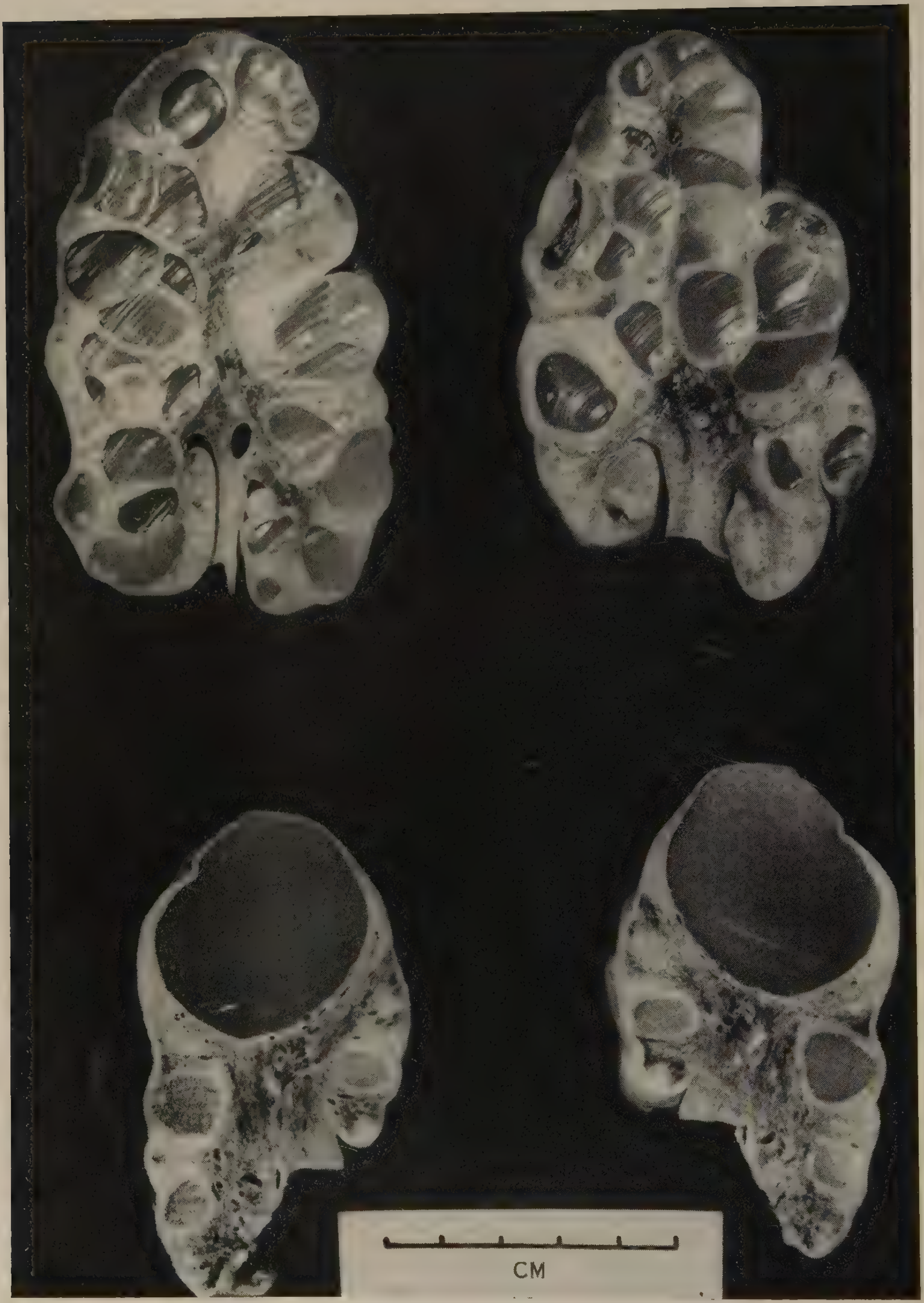

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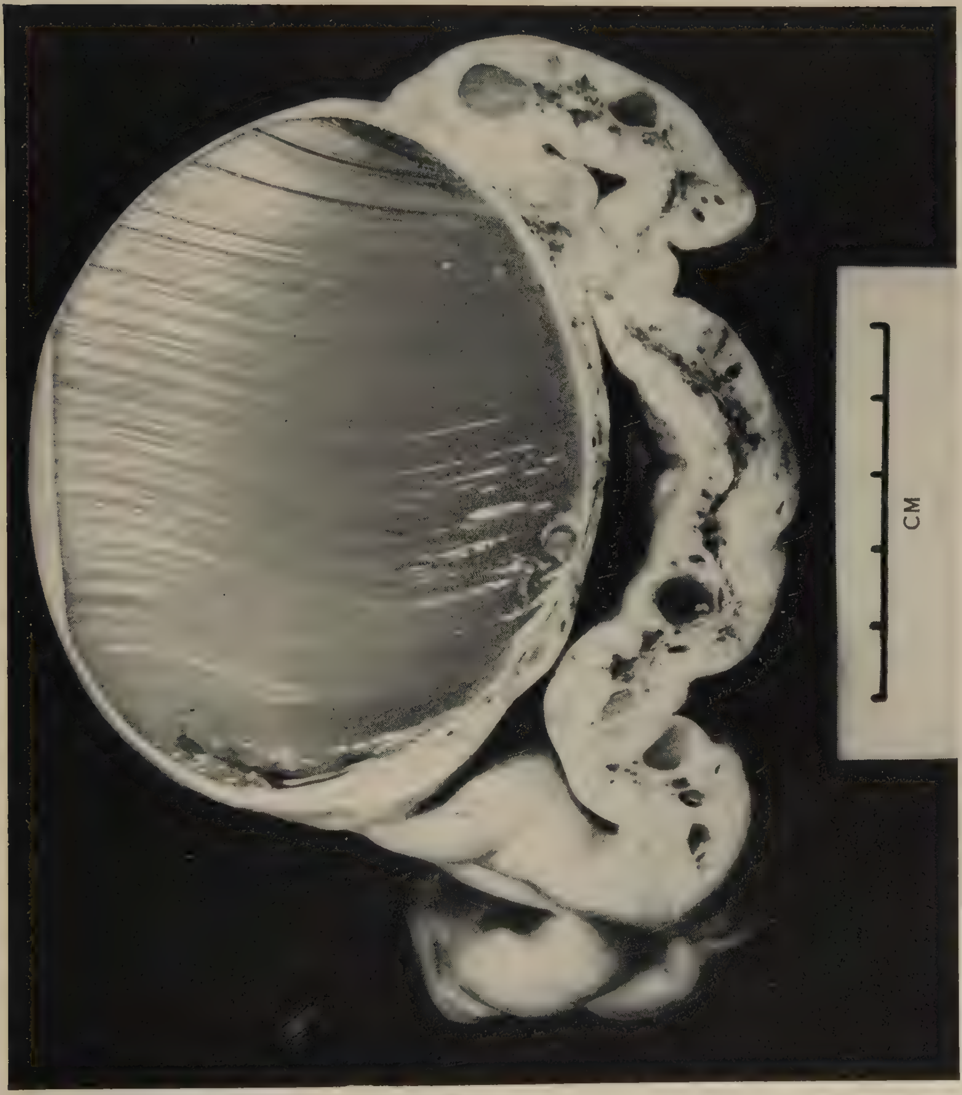

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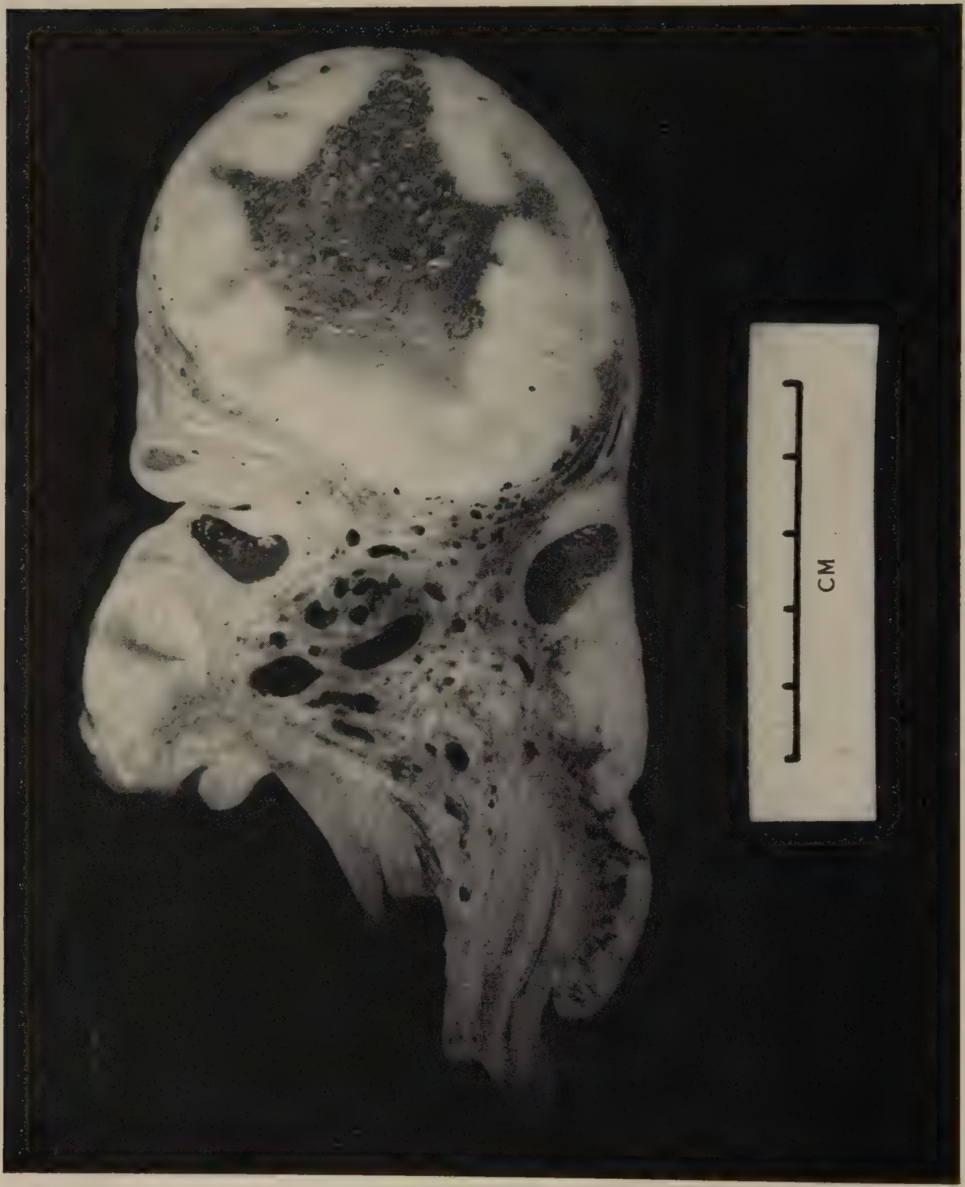

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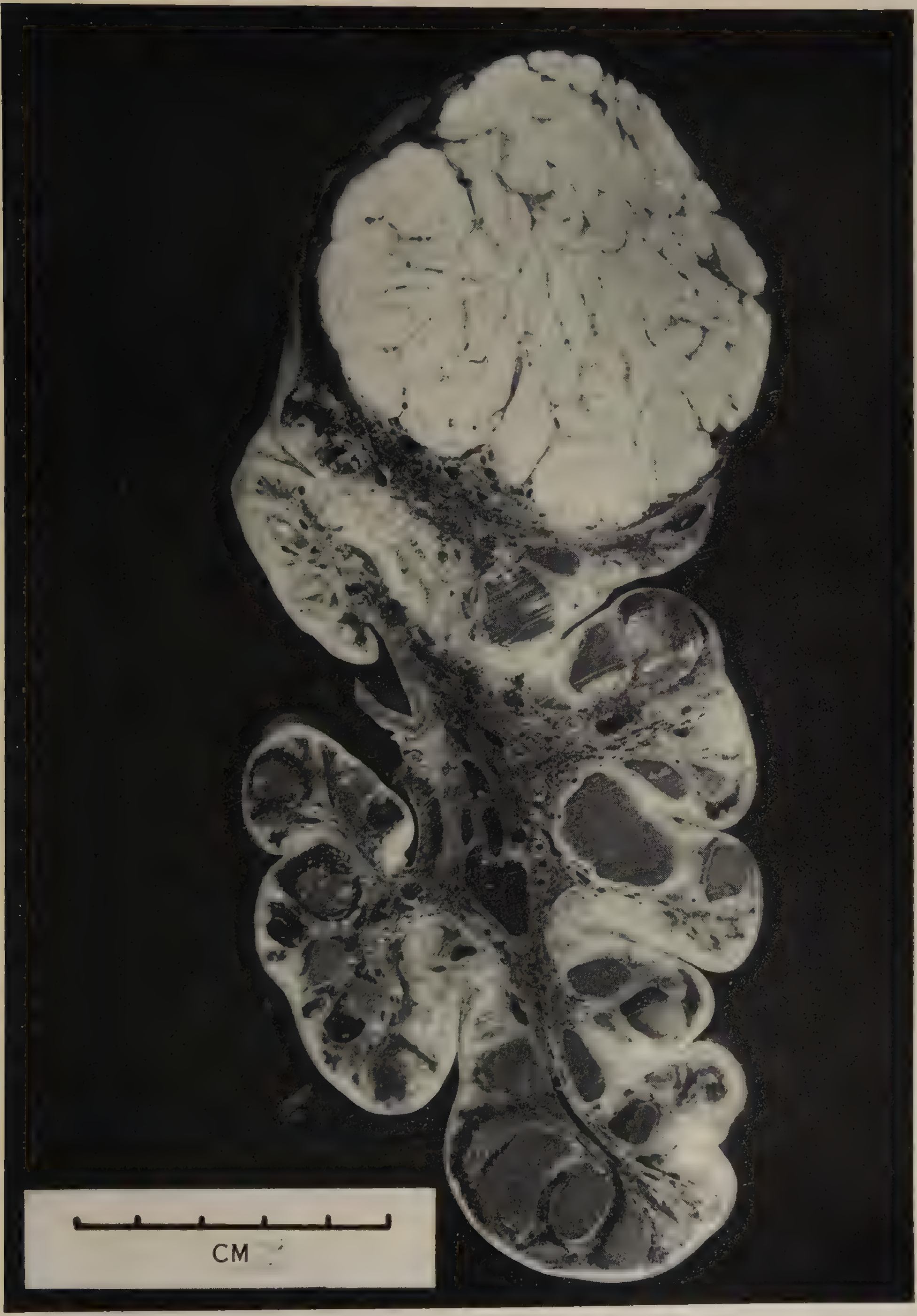

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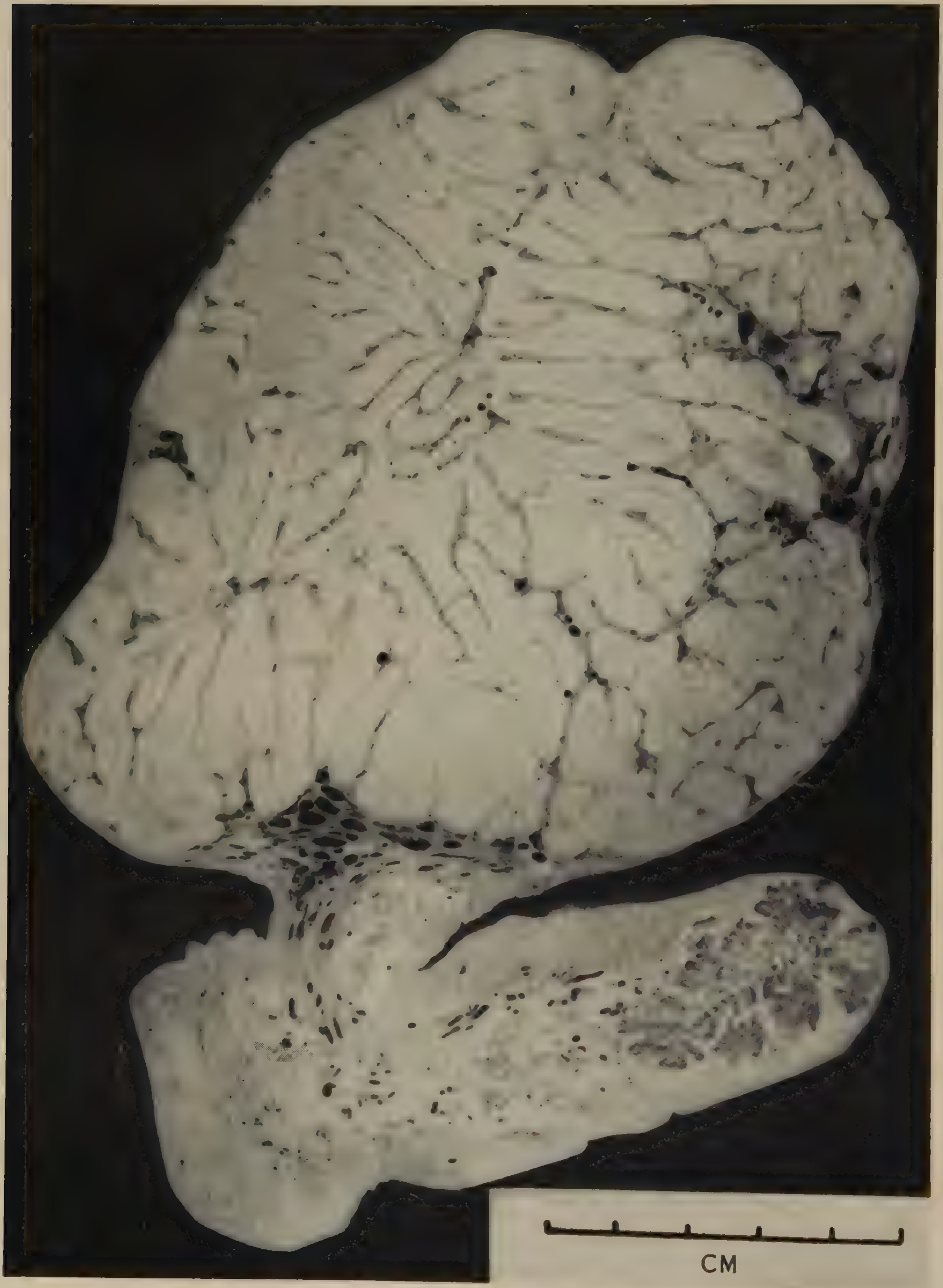

EXPLANATION OF PLATES 1-6

PLATE 1

Figs. 1, 2.—Primary oocytes in the ovaries of a late foetus 4.54 m (14 ft 11 in.) long. × 500.

Fig. 3.—Two early oocytes in an ovary of a late foetus 4.66 m (15 ft 3 in.) long, one oocyte containing three ova. × 500.

Fig. 4.—A well-developed oocyte from the ovaries of a late foetus 4.54 m (14 ft 11 in.) long. × 500.

PLATE 2

Above: sections through an immature ovary of a humpback whale within the maturing length range. Abundant Graafian follicles, the largest being 18 mm in diameter.

Below: sections through a small ovary showing one maturing Graafian follicle 38 mm in diameter.

PLATE 3

Section of an ovary of a young female humpback whale showing a mature Graafian follicle 87 mm in diameter.

PLATE 4

Section of an ovary showing a recently burst Graafian follicle (63 mm in diameter), the lining of which is beginning to fold into the gel-filled centre to form a corpus luteum. Resting follicles to 16 mm in diameter. One corpus albicans visible.

PLATE 5

Section of an ovary showing a recently formed corpus luteum 75 mm in diameter. No embryo found in the uterus. Resting follicles to 20 mm in diameter.

PLATE 6

Section of an ovary of a female humpback whale in late pregnancy. Functional corpus luteum 125 by 115 mm with depressed scar above. Parts of three corpora albicantia visible. Graafian follicles contracted to 4 mm just visible round the edges of the section.

EGGS AND LARVAE OF THE FOUR-WINGED FLYING FISH, *HIRUNDICHTHYS SPECULIGER* (VALENCIENNES)

By I. S. R. Munro*

(*Manuscript received August 8, 1953*)

Summary

The eggs of the four-winged or mirror-finned hirundine flying fish, *Hirundichthys speculiger* (Valenciennes), are spawned off the New South Wales coast in masses attached to floating objects. The eggs are heavier than sea-water and employ floating objects to buoy them at the surface. The eggs adhere by means of cords of long filaments attached to one pole of the egg membrane. Specific identification of the eggs is based on the arrangement of these filaments. A sample of naturally spawned eggs was maintained in culture for 15 days. The larvae appeared to feed on ciliate protozoans after absorption of the yolk sac. The eggs and early larvae are described and illustrated.

I. Source of Material

During the morning of February 27, 1951, a floating mass of exocoetid eggs was obtained several miles off Jibbon Point, Port Hacking, N.S.W. The mass consisted of several thousand eggs adherent by cords of tendrils to an empty pint bottle. It was placed in a laboratory aquarium tank at noon and some larvae (Plate 1, Fig. 3) hatched shortly afterwards. Some of these larvae were isolated in separate cells of celluloid and bolting silk, but all had died by the morning of March 1. On March 8, 9 days subsequent to the date of collection, two larvae were observed in a small beaker of salt water which had been used for the transport of a few eggs removed from the mass. Presumably these had hatched several days prior to discovery and were feeding on the bottom of the vessel where large ciliate protozoans were living on the putrified remains of some unhatched eggs. The vessel had been in bright sunlight and the sea-water subjected to diurnal temperature variations and evaporation. The surviving larvae were transferred to a 3-l. vessel of fresh, filtered sea-water which was changed daily and maintained at room temperature, 22.5-24.0°C. Food was provided daily, first with ciliates from the decaying eggs, and subsequently with freshly collected marine phytoplankton. One larva lived for a single day, but the other (Plate 1, Fig. 4) survived 6 days (to March 14), 15 days from the collection of the eggs.

II. Characters of the Eggs

The eggs are not perfectly spherical and range in diameter from 1.53 to 1.87 mm (mean 1.65 mm). The yolk material is transparent and tinted pale yellow in unfertilized eggs and in those containing embryos of moderate development. The colour changes to brown as development

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* Division of Fisheries, C.S.I.R.O., Cronulla, N.S.W.

proceeds, owing to a masking effect from proliferation of melanophores on the surfaces of the yolk and embryo. A cluster of minute oil globules is present at extrusion and remains during early development within the egg. Oil globules are more or less spherical in shape, hyaline in appearance, but not uniform in diameter.

The specific gravity is apparently greater than that of sea-water since the eggs sink when detached from the egg mass. As in several other exocoetid genera with non-pelagic eggs, the egg-membrane is adorned with long filaments for adhesion to, or entanglement with, floating objects. The arrangement in this instance is specialized and characteristic of known representatives of the genus *Hirundichthys*. The general arrangement is similar to that described by Bruun (1935) for *H. affinis*, but numbers differ. The filaments are grouped in disk-shaped patches at opposite poles of the egg.

At the basal pole are grouped 18-20 long filaments. These are attached to the egg membrane in a closely set cluster, occupying an area represented by a circle of diameter 0.40-0.45 mm. The filaments are approximately 5 mm long and are slightly swollen at their point of attachment to the egg membrane. They are twisted together in loose cords which measure about 0.20 mm diameter. The cords are united with those from other eggs, usually groups of six, the common stalks of each bunch tangled into the general mass of filaments adherent to the floating object.

At the distal pole of the egg are grouped about 30 rudimentary hook-like filaments. These are swollen at their point of attachment to the egg membrane and taper to fine points at their free ends. They measure 0.17-0.18 mm and, being hook-like in appearance, may function in that capacity as an additional mechanism of attachment. The area of the egg membrane to which the short filaments are attached is greater than that similarly occupied at the opposite pole, namely a circle of diameter 0.65-0.80 mm. The points of attachment are also more sparsely distributed.

III. EARLY EGG EMBRYOS

The least advanced eggs contained embryos with about 24 precaudal somites and no segmentation in the caudal region. The eyes are without pigment, but have received the lens and the choroid fissure is open. The mid brain in the region of the optic lobes is prominent and the rudiments of the auditory vesicles have appeared. The pectoral fin buds are large swellings behind the auditory vesicles. The yolk is yellowish hyaline, contains a number of small oil globules, and still occupies most of the space inside the egg membrane. Small stellate melanophores are scattered over most of the dorsal surface of the embryo, being oriented mostly in dextral and sinistral series and densest in the mid regions where the embryo is attached to the yolk. A large number of similar small melanophores is scattered over the dorsal surface of the yolk (Plate 1, Fig. 1).

IV. ADVANCED EGG EMBRYOS

The majority of the eggs were more advanced than those described above but not ready for hatching. They differ from the prehatching stages mostly in the lesser degree of pigmentation and in the shorter free extension of the body in the caudal region. The yolk had been partly absorbed and decreased in size. The brain has separate fore brain, mid brain, and cerebellum region. The choroid fissure has not closed but the eyes are pigmented externally with some scattered stellate melanophores. The auditory vesicles are still small but the pectoral fin buds are enlarged into lobes as long as the eye diameter. Over 40 somites are differentiated, of which 28 can be attributed to the precaudal region and about 14 to the caudal appendage. These numbers are in agreement with adult vertebral counts of 27 or 28 prehaemal and 17-19 haemal given by Bruun (1935) for *H. speculiger*. The heart consists of two chambers, and is functional. The blood is corpuscular and there is a particularly prominent vitelline circulatory system comprising three extremely large vessels which cross the surface of the yolk. The surface of the yolk is completely invested by a single layer of very large stellate melanophores. The embryo is pigmented in much the same manner as the earlier stage except that the melanophores are much more numerous and enlarged, although not as large as those on the yolk. There is a cluster over the mid and hind brains, and a dorso-lateral series on each side extending back not quite as far as the anus. They are concentrated mostly in the ventro-lateral sulcus, on each side, between the embryo and yolk, in the region just posterior to the pectoral fin buds (Plate 1, Fig. 2).

V. NEWLY HATCHED LARVAE

The larva at hatching measures 4.5 mm. The yolk sac is barely twice as large as the head. The fin fold of the pectoral and pelvic fins is large but that of the unpaired fins is restricted to the post-pelvic region and divided into dorsal, caudal, and anal fin regions. The three vitelline vessels persist and a number of capillaries has appeared on the caudal fin fold. The heart lies anterior to the yolk. Both the heart and the aorta are bright crimson red from the circulating blood, and the vascular vessels are pale yellowish. Owing to masking by heavy pigmentation it is impossible to count the precaudal somites but there appear to be 15-17 caudal somites now differentiated.

The pigment cells consist of large yellow chromatophores with enormous spidery melanophores superimposed upon them. The heavy pigmentation almost completely invests the body, but the distal half of the post-anal region is only sparsely covered with melanophores. The contraction of chromatophores following death gives a clearer picture of melanophore arrangement in three well-defined longitudinal series along the sides and two lateral series bordering the gut. In life the melanophores contract and expand according to the intensity of the light. The yolk is hyaline and its surface invested with orange chromatophores together with many stellate melanophores. The eyes are metallic silvery with overlying black pigment cells. The lens is hyaline, and the choroid fissure still open. The base of the pectoral fin has a few stellate melanophores. The pelvic fin bud has a single yellow cell placed centrally (Plate 1, Fig. 3).

VI. Larvae 5.7 mm Long

The larva which survived 15 days after collection of the egg mass measured 5.7 mm. The exact age is unknown since the time of hatching of this individual was not observed. It could not be more than 12 days or less than 8 days from hatching. It is characterized principally by complete absorption of the yolk and the presence of a functional mouth and gut. The pectoral and pelvic fins are also functional and the larva capable of swimming voluntarily around the vessel in search of food. The fin fold of the unpaired fins is still present in part but conspicuously divided into dorsal, caudal, and anal lobes. The pectoral, ventral, and caudal fins are equipped with supporting radials which are articulate. Their counts are respectively 17, 6 or 7, and 14 rays. The rays of the dorsal and anal fins are little more than localized thickenings of the fin fold, and are not articulate. Their counts were respectively 11 and 10 when the specimen was drawn, but a day later had increased to 13 and 12 respectively. The ventrals are inserted nearer the base of the caudal fin than to the snout, and the first anal ray originates underneath the second dorsal ray. All these characters support the diagnosis as a species of *Hirundichthys*. The body is heavily pigmented with a thick covering of melanophores over the head and trunk regions. Beneath the dorsal fin the pigmentation is less intense, consisting of relatively few isolated melanophores. Posterior to the dorsal and anal fins there is no pigment. The pectoral and ventral fins are intensely black on the rays and membranes, but the margins of the membranes are hyaline. The iris is metallic silvery (Plate 1, Fig. 4).

VII. Identification of Material

Seven genera are represented in the list of 10 species of exocoetid fishes from the Australian region. Only four species have been recorded from the Tasman Sea and New South Wales. The eggs are unlikely to belong to any of the following genera for reasons stated: *Exocoetus*—1.7-2.9 mm diameter with smooth surface (see Bruun 1935 for *E. volitans* Linnaeus; Bruun 1935 and Breder 1938 for *E. obtusirostris* Günther); *Oxyporhamphus*—2.0 mm diameter with uniformly distributed short spine-like processes (see Bruun 1935 for *O. micropterus similis* Bruun; Delsman 1924 for *"Hemirhamphus* sp." = *O. micropterus micropterus* (Valenciennes)); *Parexocoetus*—1.3-1.4 mm diameter with about 38 filaments uniformly distributed (see Breder 1927, 1932 for *P. mesogaster* (Bloch)

= *P. brachypterus littoralis* Breder); *Danichthys*—1.4-1.5 mm diameter with 80-90 uniformly distributed short filaments (see D'Ancona 1932 for *D. rondeletii* (Valenciennes)); *Cypselurus*—1.2-1.8 mm diameter with 54-114 uniformly distributed filaments (see Breder 1927, 1938 and Bruun 1935 for *C. comatus* (Mitchill); Bruun 1935 for *C. lutkeni* (Jordan and Evermann); Breder 1927 for *C. heterurus* (Rafinesque)), or 1.6-1.8 mm diameter with 14-20 filaments at one pole and a single longer filament at the opposite pole (see D'Ancona 1932 and earlier authors for "*C. heterurus*"), or 1.7-1.8 mm diameter with 7-16 greatly reduced filaments at one pole, a single stout long filament at the opposite pole, and 4-6 intermediate filaments scattered over the sides (see Nayudu 1923 for *C. coromandelensis* Hornell), or 1.6-1.7 mm diameter with 60 uniformly distributed filaments, one of which only is much prolonged (see Hubbs and Kampa 1946 for *C. californicus* (Cooper)), or 1.9-2.2 mm diameter with 18-20 long filaments grouped in cords at each pole, those at one end being coarser than those at the other (see Barnhart 1932 and Miller 1952 for an unnamed species). The eggs of *Prognichthys* are insufficiently characterized (see Bruun 1935 for *P. gibbifrons* (Valenciennes)).

The eggs undoubtedly belong to the remaining genus, *Hirundichthys*. According to Bruun (1935) the ovarian eggs of *H. affinis* (Günther) are 1.5-1.6 mm diameter with 8-12 long filaments at one pole and a disk of very short threads at the opposite pole, and those of *H. speculiger* (Valenciennes) 1.9 mm diameter with unrecognizable filament detail. The egg mass closely resembles one figured by Breder (1938) as belonging to *H. affinis*. Since the diameter is closer to that of *H. speculiger* and the filaments more numerous than in *H. affinis*, the eggs are attributed to the former species.

Whitley (1937) proposed the subspecies *H. speculiger praecox* for one Tasman Sea specimen obtained by him near Lord Howe I. and five others reported from between Auckland and Sydney by Jordan and Seale (1905). These examples differ from specimens of *H. speculiger* from King George Sound, W.A. (Valenciennes 1846), Australia, unlocalized (Günther 1866), and the coast of New South Wales between Newcastle and Port Stephens (McCulloch 1911) only in the markings on the pectoral fins. The larger amount of white on these fins is typical of juveniles in the related *H. affinis* so the status of *praecox* Whitley is doubtful.

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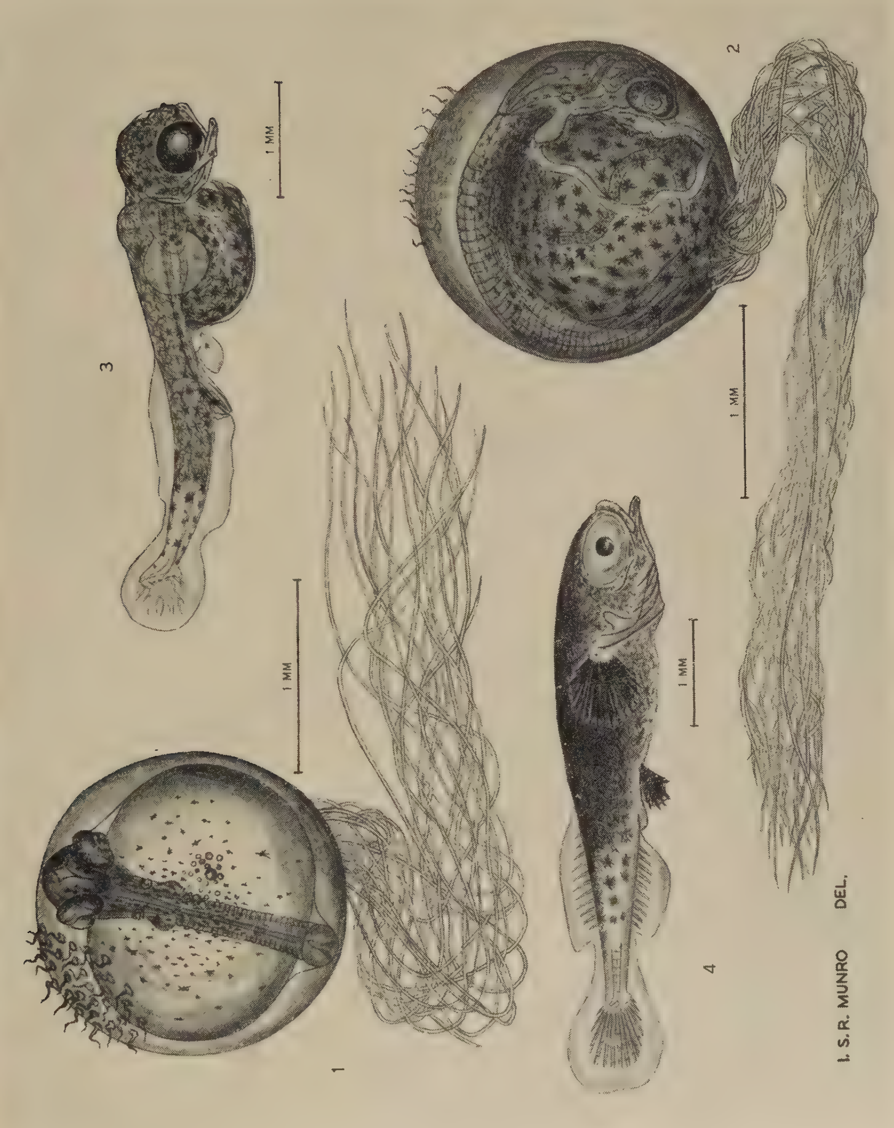
EGGS AND LARVAE OF FOUR-WINGED FLYING FISH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EXPLANATION OF PLATE 1

Eggs, larva, and postlarva of the four-winged flying fish, *Hirundichthys speculiger* (Valenciennes), from off Port Hacking, N.S.W.

Fig. 1.—Egg with early embryo of unknown age, February 28, 1951.

Fig. 2.—Egg with more advanced embryo, February 28, 1951.

Fig. 3.—Newly hatched larva, 4.5 mm, February 27, 1951.

Fig. 4.—Postlarva, 5.7 mm, March 13, 1951.

THE MUGILIDAE OF AUSTRALIA AND ADJACENT SEAS

By J. M. Thomson*

(*Manuscript received April 23, 1953*)

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Summary

Anatomical variation is slight in the Mugilidae except in the details of the mouth structures. The scales, fin rays, adipose eyelid, and stomach caecae are all useful if due regard is paid to alterations with size and age. Thirty-eight genera (excluding fossils) have been named. Of these, 13 are recognized here as valid. Seventeen species belonging to nine genera are recorded, illustrated, and fully described from Australian waters. Keys to the genera and to the Australian species are included.

I. Introduction

Since Macleay's (1880) paper on this group there has been no revision of the Australian mullets except McCulloch's (1921*a*, 1929) listing, although the taxonomy of individual species has been commented upon by various writers. The synonymy has become involved and a review of the genera in light of recent revisions by Schultz (1946) and by Smith (1948) is desirable.

The collections of mullet in the Australian Museum, Sydney, the Queensland Museum, Brisbane, the Western Australian Museum, Perth, and the Museum of the Department of Zoology of the University of Tokyo have been examined; a number of specimens have been obtained from overseas institutions, and extensive field collections have been made in various parts of Australia.

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* Division of Fisheries, C.S.I.R.O., Cronulla, N.S.W.

II. TAXONOMIC CRITERIA

It is unwise to create species upon one specimen. A range of samples is desirable. The type specimen has its undoubted uses, but if it should chance to be atypical it may lead to much later confusion. The author has attempted to examine as many specimens as possible of all species. This has sometimes been impossible owing to the rarity of the species concerned.

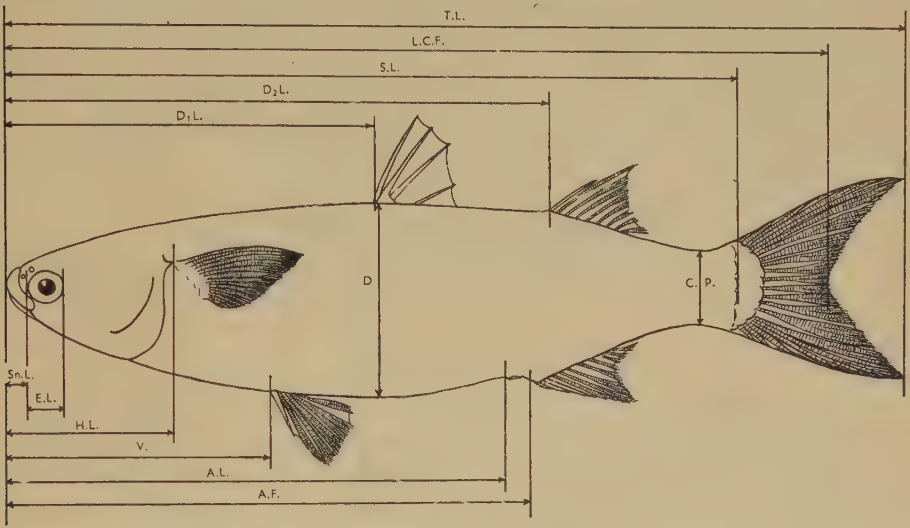

Fig. 1.—Proportional lengths of parts of the body. For significance of lettering see text.

The presence or absence of certain features, such as the axillary scale, or the adipose eyelid; the relative proportions of the body; the numbers of rays in the second and anal fins; the number of scales; the type of dentition (or its absence) ; and the features of the snout provide the main criteria of mugilid genera and species. A brief discussion of the usefulness and the variability of the features follows before the question of nomenclature and generic definition is attempted.

(*a*) *Alterations with Growth*

Many of the apparent distinctions in the published descriptions are due only to changes in relative proportions with growth. Briefly the following changes occur with age: the adipose eyelid covers more of the eye; cycloid scales of very small mullet may become ctenoid; teeth in the lips may either be lost or become so embedded in the lips that dissection is needed to find them. The mandibulary angle becomes more obtuse; the second dorsal and anal fins may become more densely scaled; various proportional measurements, particularly of axillary and obbasal scales and the interventral flange, increase. The body between the head and first dorsal origin may grow faster than the pectoral fin, which thus will not reach so far back proportionately in older fish. The depth of the body increases relative to the head length. The notch of the preorbital may become obliterated and its denticulations become blunted. Papillate lips become crenulate with age.

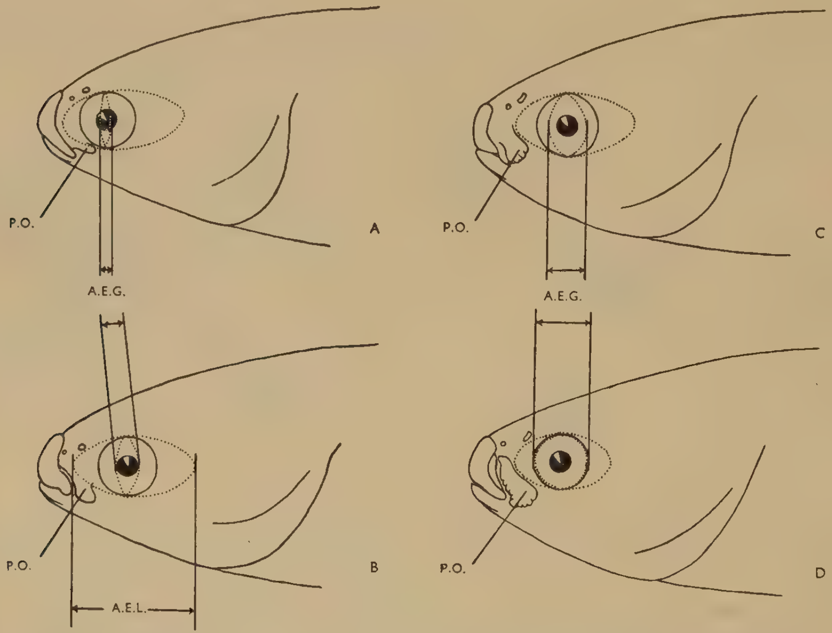

Fig. 2.—Head of mullet: *A*, *B*, *C*, show varying stages of obtrusion of the adipose tissue on the eye; in *D* the adipose eyelid is "vestigial". *P.O.*, preorbital. For other lettering see text.

(*b*) *Adipose Eyelid*

This term is a misnomer. The proportion of mullet in which it actually intrudes upon the orbit is small. Yet in most mullet the adipose membrane is present as roughly triangular deposits in front of and behind the eye. Only when the growth of this adipose membrane is such as to intrude upon the eye is it usually termed the adipose eyelid. In the literature the connotation "adipose eyelid absent" really means that the deposit is confined to the face and does not intrude upon the orbit (the genera *Joturus* and *Agonostomus* have not been sighted by the author so it may happen that the deposits are truly absent from these). "Adipose membrane" would be a better term than eyelid.

Strictly this tissue is not a third eyelid but a fatty deposition on the head which at times, but by no means always, may obtrude over the eye. In life transparent, on death it becomes opaque.

As used in most keys and descriptions the extent of the development of the adipose eyelid refers only to mature specimens. This tissue is not developed in newly hatched young and does not become apparent until a length of 4 or 5 cm, after which the area of the eye covered may continually increase during life (e.g. *Mugil cephalus* Linnaeus) or remain relatively insignificant (e.g. *Liza ramsayi* Macleay); as a consequence this feature must be used carefully (Jacot 1930). The terminology recording the extent of the development of the adipose eyelid is not very exact. The term "obsolescent" has been used by various authors to indicate merely a minute rim around the eye or by others for any stage between such a rim to a lid covering up to a third of the area, in fact anything less than the development in the type species *cephalus* has tended to be regarded as "obsolescent" or "rudimentary". In this paper "absent" will indicate that no trace of an adipose eyelid could be found. "Obsolescent" will indicate that even in the adult only a narrow rim of adipose eyelid can be distinguished, and "present" will indicate development beyond a mere rim, so as to cover a measurable portion of the eye.

(*c*) *Scales*

Both cycloid and ctenoid scales are found amongst mugilids. In young specimens of all the mullet occurring in Australian waters and probably elsewhere, the young have only cycloid scales. Ctenoid scales appear before the end of the first year in most species; though only in certain parts of the body in some cases. There may be a secondary scalation of minute cycloid scales, as described by Jacot (1920) for *Mugil cephalus*.

Schultz (1946) erred in ascribing cycloid scales to the genus *Mugil* for the type species *Mugil cephalus* Linnaeus has ctenoid scales, as described by Jacot (1920), Kesteven (1942), and Pillay (1951). The number of scales from the top of the pectoral fin to the caudal flexure is constant between small limits of variation. Behind the caudal flexure there are usually a few (2-5) scales intermediate in size between the last body scale and the minute scalation of the tail fin.

The number of scale rows counted obliquely from the origin of the first dorsal fin is also a specific character with a variation of only one or two, sometimes none. The predorsal scales, i.e. the number of scales between the first dorsal fin and the snout are given by some authors, but the scales in this region are variable and often distorted. Except where the number is easily determined no record of this attribute will be presented. The scale structure itself shows specific variation; it has been possible to examine this feature in those specimens taken in the field, but some museum specimens were not available for removal of such features for examination.

(*d*) *Axillary and Obbasal Scales*

The presence or absence of an axillary scale is another feature of use. Whitley (1945) recorded variability in this regard in *Moolgarda pura* Whitley but such occurrences must be rare. No such atypical specimens of any species were encountered during this investigation. The term axillary is here reserved for the elongated scale occurring in the axil of the pectoral fins. The elongated scales occurring at the base of the first dorsal and ventral fins will be termed the dorsal and ventral obbasals. The presence or absence of these and their relative sizes are recorded.

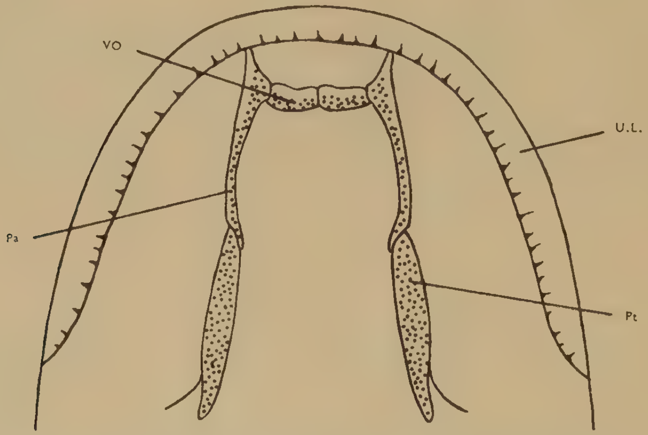

Fig. 3.—Upper roof of mouth, showing position of *Pa*, palatine; *Pt*, pterygoid; *U.L.*, upper lip; *VO*, vomer.

(*e*) *Interventral Flange*

Between the ventral fins is an elongately triangular arrangement of scales to which Smith (1935) has drawn attention. Smith's suggestion that the arrangement of the ventral fins and the interventral flange may have specific or generic usefulness could not be entirely tested as many museum specimens proved to be damaged in this region when the body was slit to allow formalin to penetrate the body cavity. However, some variation was noted; on the other hand other species showed similar arrangement, nor was any proper correlation found with generic limits established on other grounds. The relative distance along the fins reached by the apical scale of the flange has specific usefulness.

(*f*) *Fins*

The spines and rays of the pectoral and ventral fins are constant in the family. The numbers of rays in the second dorsal and anal fins are much more constant within the species than in most families of fish, but even here exceptional specimens show one ray more or less than the usual.

The fact that variations have not been found in some species may merely indicate that only a small number of specimens has been examined. The first dorsal fin is rarely scaled, but the others are in some species, the relative size of the scales, and the area covered by them helping to diagnose the species. Museum specimens are often unsatisfactory in this regard, the scales sometimes being lost, as is shown by the comparison with fresh specimens in the field. The caudal fin rays vary in number, but it is impossible to count the small lateral rays of many species without dissection, and specimens available only from museum collections could not be so treated. Consequently this feature is not used to any extent in the specific descriptions.

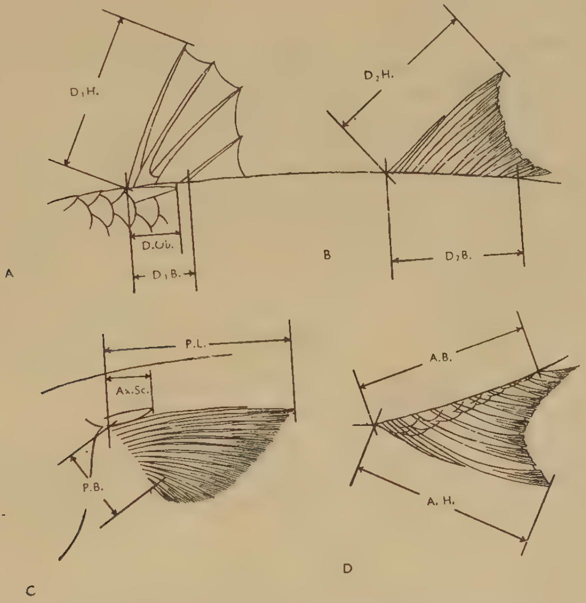

Fig. 4.—*A*, first dorsal fin; *B*, second dorsal fin; *C*. pectoral fin; *D*, anal fin. For significance of lettering see text.

(*g*) *Dentition and Characters of the Lips*

The lips may be narrow or thick, smooth or lamellate or papillate. The upper lip may be terminal or it may be overhung by a projection of the snout. There is disagreement concerning the nature of the cilia which occur on the lip of some mugilids. These always occur in species where no obvious teeth are present, and Schultz (1946) appears to be correct in regarding them as much reduced ciliform teeth. They certainly appear so under the microscope. The ciliform or setiform teeth may be simply tipped or they may be bifid, trifid, or even multicuspid. In various genera denticular patches may occur on one or more of the vomers, palatines, pterygoids, tongue, and pharyngeal pads.

(*h*) *Features of the Head*

The preorbital is usually denticulate, but the relative size and number of the denticulations may vary. It may also have its anterior edge notched, curved, or straight. This bone is variously broad or narrow.

The nostrils may be variously placed. The posterior is usually above the level of the eye, but in some species it is below the upper edge of the eye. In different species the two nostrils may be closer to each other than the anterior is from the edge of the upper lip or the posterior from the eye or they may be further apart than one or both these distances. The posterior nostril is usually lunate in shape, but is reported as being round in some species.

The maxillary and premaxillary may be almost straight or may bend downwards posteriorly. When the latter occurs, the posterior end of the maxilla is usually visible when the mouth is closed.

The eye may be greater or less than the snout in length. This is slightly variable, but the range in size is not great. Thus an eye which is only slightly shorter than the snout may in other specimens of the same species be equal to or even longer than the snout. But an eye markedly different in length from the snout is constantly so. The distance behind and before the eye which the adipose eyelids may cover differs between species; this and the distance of the gap in the adipose lid over the eye vary with age, but are useful for distinguishing mature specimens.

The interorbital distance is variable, the broad-headedness of the mullet being variously developed.

The gular or interopercular space and the head profiles are not very useful characters, except for extreme cases such as the extraordinary profile of *Rhinomugil;* the details of these features being altered by the degree of contraction of the muscles.

(*i*) *Relative Proportions*

Various body proportions have been found to have a usefulness which varies from species to species. It is not intended to mention all those used, which may be seen in the tables and descriptions below, but some commentary on certain points is warranted. The mandibulary angle is stressed as a generic criterion by some authors. This angle is relatively constant in some species; but it varies with age in others. For instance, this angle is acute in young specimens of *Mugil cephalus*, gradually approaches a right angle at a length about 32 cm, and thereafter increases to an oblique angle.

Some proportions of the body, for example the depth of the caudal peduncle, are affected by compression in storage or by distortion during preservation.

The relative lengths of the pectoral fins have some generic and specific importance, and the place of origin of the dorsal fins is distinctive.

(*j*) *Measurements and Records*

The total length, the length to the caudal fork, the standard length (length to the caudal flexure), and the anal length have been measured between parallels on a measuring board. All other measurements have been made by the use of dividers. It is unfortunate that many workers have not recorded their methods of measuring nor do they define their terms. As a result differences in recorded relative proportions may not be true but a result of different techniques. The measurements of fin distances between parallels will obviously give somewhat varying results from measurements done by dividers. The latter are preferable for all but over-all measurements because of the visual difficulty of measuring accurately the perpendiculars of a bulky fish.

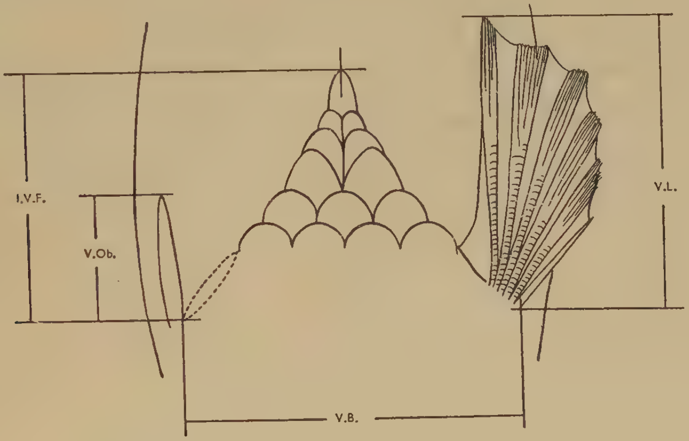

Fig. 5.—Under side of body, left ventral fin cut away showing ventral fin, the ventral obbasal scale, and the interventral flange. For significance of lettering see text.

Royce (1942), Carlander and Smith (1945), and Ricker and Merriman (1945) have discussed the use of various length measurements and the various meanings which different workers have given to the terms total length and standard length. It is the author's contention that, for mullet at least, the length to the caudal fork is the most satisfactory measurement as the outer caudal rays are frequently frayed and broken off for greater or less lengths, particularly in long-preserved and frequently handled specimens. The standard length is difficult to determine exactly and the term has been applied to somewhat different measurements (Carlander and Smith 1945). In mullet it is difficult to determine either the precise beginning of the tail or the end of the trunk vertebrae. In practice the distance to the last row of large body scales has been measured.

Most authors compare the main body proportions to the total length (though it should be noted that total length does not always mean to the end of the longest caudal ray. Smith 1935 used the length to the caudal fork, though he termed it total length). For the sake of comparison both proportions to both total length and to length to the caudal fork will be given in this paper. The methods of measuring standard length vary too much to warrant using this as a measure. The details of the proportional measurements for each species will be recorded in tabular form, only the outstanding features being mentioned in the specific descriptions (Appendix I). Certain measurements are so constant that only exceptional species differ from them.

The following are the proportional measurements which will be compared to the standards named, with the symbols used for them in Table 3 and the text. In the tables where the relationship to both total length and to length to the caudal fork are expressed, the term T.L. only will be used and the figures in brackets after the total length ratio should be understood to refer to the ratio in terms of the L.C.F.

(1) Measurements compared with total length:
Length to the caudal fork (T.L./L.C.F.)
Standard length (T.L./S.L.)
Length to anus (T.L./A.L.)
Length to anal fin origin (T.L./A.F.)
Depth (T.L./D.)
Head length (T.L./H.L.)
First dorsal origin (T.L./D_1)
Second dorsal origin (T.L./D_2)
Ventral origin (T.L./V.)

(2) Measurements compared with depth:
Least depth of caudal peduncle (D./C.P.)
Depth at pectoral origin level (D./P.F.)
Height of 1st dorsal fin (D./D_1H.)
Height of 2nd dorsal fin (D./D_2H.)
Height of anal fin (D./A.H.)

(3) Measurements compared with head length:
Snout length (H.L./Sn.L.)
Eye length (H.L./E.L.)
Head width (H.L./H.W.)
Mouth width (H.L./M.W.)
Interorbital width (H.L./I.O.)
Height of 1st dorsal fin (H.L./D_1H.)
Height of 2nd dorsal fin (H.L./D_2H.)
Height of anal fin (H.L./A.H.)
Length of pectoral fins (H.L./P.L.)
Length of ventral fins (H.L./V.L.)
Length from posterior to anterior edge of adipose eyelid (H.L./A.E.L.)

(4) Measurement compared with eye length:
Gap between anterior and posterior adipose eyelid (E./A.E.G.)

(5) Measurement compared with height or length of adjacent fin:
Length of the base of the 1st dorsal fin (D_1H./D_1B.)

Length of the base of the 2nd dorsal fin ($D_2H./D_2B.$)
Length of the base of the anal fin (A.H./A.B.)
Width of the base of the pectoral fin (P.L./P.B.)
Width of the ventral base (V.H./V.B.)
Length of the axillary scale (P.L./Ax.Sc.)
Length of the dorsal obbasal scale ($D_1H./D.Ob.$)
Length of the ventral obbasal scale (V.L./V.Ob.)
Length of the interventral flange (V.L./I.V.F.)

Some of these measurements are self-explanatory, but it is wise to comment on others in the interest of clearness. The depth is the greatest depth of the body, excluding fins; it is usually a little in advance of the origin of the first dorsal fin. The head length is measured from the tip of the snout to the hindmost portion of operculum. The origins of the fins are measured from the snout to the base of the first spines when these are raised at right angles. The snout is measured from the front rim of the eye to the anteriormost tip of the head. The eye length is taken as the distance between the posterior and anterior rims, which are distinguishable even in mullet with a heavy deposit of adipose eyelid tissue in life and shortly after death and is usually revealed by a gentle pressure in preserved specimens.

The interorbital width is variously defined but in the present study it has been taken as the distance measured by dividers across the head between the uppermost rims of the eye. The fin heights have been measured from the fin origin to the end of the longest ray or spine.

The base of the first dorsal fin is taken as the distance from the anterior side of the base of the first spine to the posterior side of the base of the fourth spine. This is preferred to measuring to the posterior end of the fin membrane as this is almost impossible to determine in many long-preserved specimens. The width of the ventral base is measured from the outer side of the base of one ventral fin to that of the other. The axillary scale, the obbasals, and the interventral flange are measured from the origins of their respective fins to their tip.

III. THE GENERA OF MULLETS

The family Mugilidae consists of members of the Mugilformes (or Percesoces) distinguished by having the pelvic bones connected with the post-cleithra by a ligament. Vertebrae 24-26 (usually 24) (Berg 1940).

They are distinguishable externally by having 2 separate dorsal fins, of which the 1st is formed of 4 spines, the ventrals are abdominal but not far back and have 1 spine and 5 rays and the opercles are without spines. The anal fin has 3 spines (2 in the young querimana stage). The teeth, when present, are minute. No lateral line.

Thirty-eight genera of mullets (excluding fossils) have been named. They are listed in Table 1 with their authors, the genotype, and the genus to which they are allotted here. Thirteen genera are recognized as valid.

TABLE 1

NOMINAL GENERIC NAMES OF MULLET IN CHRONOLOGICAL ORDER OF DESIGNATION

Genus	Author	Date	Genotype	Genus to Which Allotted
1. *Mugil*	Linnaeus	1758	*M. cephalus* Linnaeus	*Mugil*
2. *Cephalus*	Lacepede	1800	*Mugil cephalus* Linnaeus	*Mugil*
3. *Agonostomus*	Bennett	1832	*A. telfairii* Bennett	*Agonostomus*
4. *Cestraeus*	Cuvier & Valenciennes	1836	*C. plicatilis* Cuvier & Valenciennes	*Cestraeus*
5. *Dajaus*	Cuvier & Valenciennes	1836	*Mugil monticola* Bancroft	*Agonostomus*
6. *Nestis*	Cuvier & Valenciennes	1836	*N. cyprinoides* Cuvier & Valenciennes	*Agonostomus*
7. *Arnion*	Gistel	1848	*Mugil cephalus* Linnaeus	*Mugil*
8. *Ello*	Gistel	1848	?*Mugil cephalus* Linnaeus	*Mugil*
9. *Joturus*	Poey	1860	*J. pichardi* Poey	*Joturus*
10. *Myxus*	Gunther	1861	*Mugil elongatus* Gunther	*Myxus*
11. *Chaenomugil*	Gill	1863	*Mugil proboscidens* Gunther	*Chaenomugil*
12. *Rhinomugil*	Gill	1863	*Mugil corsula* Hamilton	*Rhinomugil*
13. *Gonostomyxus*	MacDonald	1869	*G. loa-loa* MacDonald	*Cestraeus*
14. *Neomyxus*	Steindachner	1878	*Myxus* (*Neomyxus*) *sclateri* Steindachner	*Chaenomugil*
15. *Querimana*	Jordan & Gilbert	1883	*Myxus harengus* Gunther	*Myxus* (partim) *Mugil* (partim)
16. *Aeschrichthys*	Macleay	1883	*A. goldiei* Macleay	*Cestraeus*
17. *Liza*	Jordan & Swain	1884	*Mugil capito* Cuvier	*Liza*
18. *Trachystoma*	Ogilby	1887	*T. multidens* Ogilby (= *Mugil petardi* Castelnau)	*Trachystoma*
19. *Neomugil*	Vaillant	1894	*Mugil digueti* V. (=*M. monticola* Bancroft)	*Agonostomus*
20. *Oedaleschilus*	Fowler	1903	*Mugil labeo* Cuvier	*Liza*
21. *Squalomugil*	Ogilby	1908	*Mugil nasutus* de Vis	*Rhinomugil*
22. *Xenorhynchichthys*	Regan	1908	*Joturus stipes* Jordan & Gilbert	*Joturus*
23. *Chelon*	Jordan & Evermann	1917	*Mugil chelo* Cuvier	*Liza*
24. *Ellochelon*	Whitley	1930	*Mugil vaigiensis* Quoy & Gaimard	*Liza*
25. *Protomugil*	Popov	1930	*Mugil saliens* Risso	*Liza*
26. *Sicamugil*	Fowler	1939	*Mugil hamiltoni* Day	*Trachystoma*
27. *Gracilimugil*	Whitley	1941	*Mugil ramsayi* Macleay	*Liza*
28. *Moolgarda*	Whitley	1945	*Moolgarda pura* Whitley	*Liza*
29. *Planiliza*	Whitley	1945	*Moolgarda* (*Planiliza*) *ordensis* Whitley	*Liza*
30. *Aldrichetta*	Whitley	1945	*Agonostomus forsteri* (Cuvier & Valenciennes)	*Aldrichetta*

TABLE 1 (*Continued*)

Genus	Author	Date	Genotype	Genus to Which Allotted
31. *Xenomugil*	Schultz	1946	*Mugil thorburni* Jordan & Starks	*Xenomugil*
32. *Crenimugil*	Schultz	1946	*Mugil crenilabis* Forskal	*Crenimugil*
33. *Heteromugil*	Schultz	1946	*Mugil tricuspidens* Smith	*Heteromugil*
34. *Oxymugil*	Whitley	1948	*Mugil acutus* (Cuvier & Valenciennes)	*Mugil*
35. *Pteromugil*	Smith	1948	*Mugil diadema* Gilchrist & Thompson	*Aldrichetta*
36. *Strializa*	Smith	1948	*Mugil canaliculatus* Smith	*Liza*
37. *Valamugil*	Smith	1948	*Mugil seheli* Forskal	*Valamugil*

The mullets are remarkably uniform in external anatomy. The principal criteria of the genera are the mouth-parts, as Schultz (1946) has made clear. Of these the more important seem to be the nature of the upper attachment of the maxilla, and the curvature of its posterior end, together with its degree of exposure; the distribution and nature of the teeth; the relative thickness of the lips and the degree of papillation; the inferior or terminal position of the mouth; and the presence or absence of the symphysial knob. The more easily discernible features are compared in Table 2.

TABLE 2

COMPARISON OF MOUTH-PARTS OF MUGILID GENERA

X = present; O = absent; ? = unknown (material lacking)

	Mugil	*Liza*	*Agonostomus*	*Joturus*	*Cestraeus*	*Chaenomugil*	*Xenomugil*	*Crenimugil*	*Aldrichetta*	*Myxus*	*Trachystoma*	*Valamugil*	*Rhinomugil*
Upper lip thick	O	O	X	X	X	X	X	X	O	O	O	O	O
Lower lip thick	O	O	X	X	X	X	X	X	O	O	O	O	O
Lower lip folded down	O	O	O	O	X	X	X	X	O	O	O	O	O
Lips papillate	O	O	O	O	O	X	O	X	O	O	O	O	O
Lips with lamellae and fleshy lobes to mandible	O	O	O	O	X	O	O	O	O	O	O	O	O
Lips terminal	X	X	?	O	X	X	X	X	X	X	X	X	O
Premaxillary hooked down	O	X	O	O	O	O	O	X	O	O	O	O	O
Maxillary hooked down	O	X	O	O	O	O	O	X	O	O	O	X	O
End of maxillary exposed	O	X	O	O	O	O	O	O	O	O	O	O	O
Symphysial knob	X	X	O	O	X	O	X	X	X	X	X	X	X
Teeth in upper jaw	X	X	X	X	X	X	X	O	X	X	X	X	X
Teeth in lower jaw	X	X	X	X	X	X	X	O	X	X	X	X	X
Teeth on vomers	O	XO	X	X	X	O	O	O	X	X	X	O	O
Teeth on palatine	O	XO	X	X	O	O	O	X	X	X	X	O	O
Teeth on pterygoid	O	X	?	?	O	O	O	O	X	O	X	X	O
Teeth on tongue	O	X	O	X	O	X	O	X	X	O	X	X	O

KEY TO GENERA OF THE FAMILY MUGILIDAE

1. Two or 4 bluntly rounded fleshy lobes, free posteriorly, at the latero-posterior end of the mandible 2 strips of transverse, close-set, membranous lamellae along each side of lower jaw externally .. .. *Cestraeus**
Mandible without the fleshy lobes and lamellae 2
2 (1). Upper lip not forming anterior tip of head, but inferior to a fleshy snout 3
Upper lip forming anterior tip of head, not inferior to the snout 4
3 (2). Eyes lateral, dorsal edge of orbit below interorbital region of head; a band of incisor-like multicuspid teeth in each jaw — interrupted medianly in the lower jaw. Palate and tongue with teeth .. .. *Joturus*
Eyes dorso-lateral; dorsal edge of orbit above interorbital region. A single row of simple ciliform teeth in both lips. Palate and tongue toothless .. .. *Rhinomugil**
4 (2). Maxilla markedly exposed posteriorly when the mouth is closed .. .. .. *Liza**
Maxilla not exposed posteriorly 5
5 (4). No symphysial knob at tip of lower jaw, lips thick 6
A symphysial knob at tip of lower jaw 7
6 (5). Teeth on tongue but not on vomers and palatines .. .. *Chaenomugil*
Teeth on vomers and palatines but not on tongue .. .. *Agonostomus*
7 (5). Lips thick, lower lip directed downwards 8
Lips not thick, lower lip directed horizontally, not directed downwards .. 9
8 (7). Lips papillate, crenulate in adults, both lips toothless. Adipose eyelid obsolescent .. .. *Crenimugil**
Lips not papillate, lips with teeth, adipose eyelid well developed . *Xenomugil*
9 (7). No teeth on vomers, palatines, pterygoids, or tongue; adipose eyelid well developed .. .. *Mugil**
Teeth at least on some of the palate bones, adipose eyelid obsolescent .. 10
10 (9). Maxillary curved down posteriorly; teeth on pterygoids and tongue, but not on vomers and palatine .. .. *Valamugil**
Maxillary not curved down, teeth on vomers and palatines 11
11 (10). No teeth on pterygoids and tongue .. .. *Myxus**
Teeth on pterygoids and tongue 12
12 (11). Scales ctenoid, 1 row of feeble teeth on lips; no teeth on pharyngeal pad or gullet .. .. *Trachystoma**
Scales cycloid; strong teeth in a band along both lips; numerous teeth on pharyngeal pads and gullet .. .. *Aldrichetta**

The following definitions largely follow Schultz (1946).

1. Genus MUGIL Linnaeus

Mugil Linnaeus, 1758.

Mouth terminal; lips thin, the lower projecting horizontally, but not folded downwards; the teeth are ciliform or setiform in 1 or more rows and tend to be lost or embedded in the lips in older fish, the outermost row are simple-tipped, the inner bifid or trifid; no papillae, lamellae, or posterior folds in the lips. A symphysial knob at the tip of the lower jaw. The preorbital is moderately narrow, denticulate, and may be notched or straight along the anterior edge; maxillary not fixed anteriorly; maxilla and premaxilla not hooked downwards posteriorly; maxillary hidden

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* Australian genera.

TABLE 3

PROPORTIONAL MEASUREMENTS

	Mugil cephalus	*Mugil georgii*	*Liza strongylo-cephalus*	*Liza argentea*	*Liza dussumieri*	*Liza diadema*	*Liza ramsayi*	*Liza vaigiensis*	*Valamugil seheli*	*Valamugil buchanani*	*Trachy-stoma petardi*	*Aldrichetta forsteri*	*Myxus elongata*	*Crenimugil crenilabis*	*Crenimugil labiosus*	*Cestraeus goldiei*	*Rhino-mugil nasutus*
T.L./L.C.F.	1.06-1.13	1.05-1.07	1.06-1.13	1.05-1.10	1.06-1.11	1.07-1.11	1.08-1.12	1.02-1.06	1.06-1.16	1.11-1.16	1.08-1.13	1.08-1.10	1.04-1.07	1.09-1.10	1.07-1.11	1.09-1.10	1.02
T.L./S.L.	1.22-1.33	1.23-1.35	1.27-1.32	1.29-1.32	1.25-1.31	1.24-1.28	1.27-1.33	1.23-1.27	1.25-1.36	1.27-1.32	1.17-1.39	1.22-1.25	1.21-1.25	1.25-1.27	1.27-1.29	1.28-1.29	1.23
	1.14-1.19	1.17-1.22	1.14-1.23	1.15-1.23	1.15-1.20	1.16-1.17	1.16-1.21	1.19-1.23	1.13-1.20	1.22-1.26	1.04-1.21	1.12-1.15	1.12-1.19	1.15-1.16	1.16-1.21	1.17	1.20
T.L./A.L.	1.76-1.89	1.80-1.88	1.80-1.95	1.79-1.93	1.79-1.93	1.87-1.93	1.78-1.90	1.72-1.80	1.82-1.95	1.78-1.80	1.82-1.93	1.84-1.93	1.66-1.84	1.81-1.85	1.81-1.88	1.94-1.97	1.82
	1.61-1.72	1.72-1.75	1.70-1.83	1.61-1.80	1.51-1.73	1.73-1.74	1.61-1.68	1.61-1.76	1.55-1.71	1.68-1.70	1.61-1.70	1.70-1.77	1.50-1.70	1.61-1.69	1.61-1.76	1.78-1.80	1.75
T.L./D.	4.32-5.51	4.08-4.64	4.16-5.50	4.03-4.79	4.10-5.18	4.31-4.65	4.54-4.76	4.76-4.81	4.66-5.30	4.23-4.34	4.51-5.29	4.53-4.69	3.51-4.47	4.59-4.82	4.58-4.73	4.80-4.95	5.60
	4.00-5.18	3.91-4.36	4..4-4.92	3.62-4.24	3.66-4.65	3.88-4.16	4.20-4.40	4.53-4.69	4.00-5.00	4.00-4.12	4.04-4.81	4.10-4.30	3.27-4.27	4.15-4.37	4.14-4.27	4.41-4.50	5.47
T.L./H.L.	4.24-5.54	4.93-5.22	4.50-5.41	3.62-4.79	4.20-5.18	4.25-5.60	4.10-4.66	4.48-4.76	4.14-5.56	4.45-4.50	4.71-6.22	4.37-5.12	3.62-4.87	5.09-5.13	5.14-5.18	5.33-5.36	4.76
	3.91-5.01	4.66-4.87	3.07-5.00	3.37-4.24	3.85-4.74	3.94-5.05	3.79-4.12	4.21-4.64	3.78-4.94	4.16-4.25	4.33-5.07	3.96-4.27	3.37-4.52	4.61-5.00	4.61-4.86	4.73-4.89	4.65
T.L./D$_1$	2.27-2.79	2.26-2.39	2.32-2.68	2.15-2.30	2.15-2.59	2.29-2.47	2.20-2.25	2.24-2.40	2.43-2.66	2.32-2.54	2.31-2.52	2.35-2.41	2.22-2.33	2.45-2.54	2.27-2.29	2.61-2.68	2.33
	2.05-2.59	2.13-2.20	2.12-2.42	1.99-2.07	1.97-2.33	2.23-2.30	1.99-2.03	2.18-2.26	2.17-2.40	2.19-2.51	2.04-2.26	2.13-2.22	2.07-2.23	2.22-2.32	2.13-2.15	2.37-2.46	2.28
T.L./D$_2$	1.48-1.75	1.57-1.68	1.70-1.82	1.60-1.68	1.62-1.73	1.64-1.67	1.63-1.67	1.61-1.64	1.69-1.82	1.56-1.63	1.64-1.73	1.62-1.71	1.61-1.68	1.59-1.73	1.59-1.63	1.73-1.77	1.54
	1.37-1.60	1.48-1.58	1.59-1.67	1.48-1.54	1.45-1.55	1.53-1.55	1.48-1.51	1.51-1.54	1.51-1.61	1.47-1.54	1.45-1.51	1.47-1.56	1.49-1.61	1.49-1.65	1.49-1.53	1.59-1.61	1.51
D./Pect. D.	2.18-2.80	2.10-2.44	1.83-2.27	1.88-2.80	1.73-2.18	2.00-2.36	1.83-2.08	1.79-2.20	2.09-2.24	2.38-2.42	2.20-2.25	2.38-3.00	2.65-4.43	2.05-2.19	2.41-2.50	2.11-2.18	1.81
D./D. Pect.	1.03-1.28	1.20-1.42	1.10-1.19	1.09-1.28	1.10-1.23	1.22-1.24	1.19-1.25	1.13-1.25	1.18-1.28	1.19-1.25	1.13-1.35	1.14-1.28	1.14-1.38	1.14-1.19	1.17-1.25	1.12-1.20	1.38
D./D$_1$H.	1.57-2.05	2.00-2.44	1.47-1.92	1.75-1.90	1.35-1.76	1.57-1.80	1.39-1.77	1.56-1.79	1.56-2.09	1.54-1.67	1.35-1.59	1.86-2.25	2.10-2.69	1.74-1.91	1.75-1.76	1.58-1.74	1.90
D./D$_2$H.	1.52-2.29	1.75-2.10	1.22-1.67	1.73-2.13	1.28-1.85	1.52-1.87	1.57-1.66	1.39-1.58	1.23-1.60	1.42-1.50	1.50-1.78	1.50-2.07	1.91-2.86	1.58-1.61	1.38-1.43	1.52-1.56	1.29
H.L./Sn.L.	3.93-5.84	4.08-5.14	4.80-6.00	2.66-4.71	4.50-5.50	4.71-5.57	4.14-4.67	4.17-4.43	4.50-5.55	4.86-5.33	3.75-3.78	3.22-4.57	3.33-3.66	4.16-4.93	4.21-4.82	3.18-3.49	5.87
H.L./E.L.	3.45-4.31	3.46-4.00	3.22-4.00	3.20-4.70	3.37-4.22	2.86-4.71	3.62-3.73	3.51-5.10	3.37-4.33	3.20-3.31	3.33-4.53	3.05-5.14	4.23-5.00	2.30-4.14	2.50-3.53	3.50-5.00	5.22
H.L./H.W.	1.33-1.52	1.44-1.66	1.36-1.54	1.68-1.77	1.40-1.63	1.33-1.73	1.80-1.93	1.92-2.01	1.38-1.58	1.69-1.78	1.41-1.54	1.63-1.70	1.55-1.71	1.32-1.33	1.41-1.55	1.48-1.52	1.34
H.L./I.O.	1.78-2.27	2.35-2.58	1.93-2.33	2.35-3.93	2.00-2.39	1.82-2.44	2.54-2.90	1.78-1.96	2.04-2.25	2.25-2.28	2.04-2.31	2.45-3.05	2.29-3.10	1.87-1.92	2.16-2.41	2.00-2.20	4.27
H.L./D$_1$H.	1.73-2.26	1.71-2.14	1.51-1.70	1.17-2.00	1.39-1.94	1.25-1.88	1.61-1.80	1.56-1.92	1.53-1.94	1.45-1.53	1.15-1.30	1.93-2.25	1.94-2.11	1.53-1.70	1.49-1.56	1.46-1.57	2.24
H.L./D$_2$H.	1.67-2.10	1.50-1.78	1.30-1.54	1.38-2.29	1.28-1.73	1.25-1.96	1.60-1.93	1.39-1.70	1.10-1.60	1.33-1.38	1.21-1.67	1.74-2.07	1.87-2.06	1.38-1.45	1.23-1.34	1.40-1.41	1.52
H.L./A.H.	1.54-2.00	1.32-1.71	1.21-1.48	1.51-2.00	1.23-1.64	1.33-1.51	1.45-1.47	1.25-1.39	1.10-1.48	1.33-1.38	1.12-1.43	1.12-1.93	1.55-1.93	1.28-1.37	1.26-1.34	1.19-1.20	1.57
H.L./P.L.	1.02-1.77	1.06-2.00	0.86-1.11	1.34-1.77	1.10-1.43	0.92-1.51	1.36-1.45	1.08-1.31	0.79-1.45	1.33-1.40	1.07-1.43	1.23-1.50	1.41-1.58	1.01-1.06	1.00-1.06	1.04-1.17	1.02
H.L./V.L.	1.56-2.11	1.44-1.63	1.32-1.61	1.51-2.66	1.34-1.69	1.17-1.74	1.60-1.91	1.39-1.62	1.34-1.77	1.37-1.42	1.09-1.30	1.51-2.63	1.77-1.93	1.50-1.54	1.35-1.49	1.19-1.34	1.52
E./A.E.G.	2.12-4.30	1.58-1.85	1.14-1.80		1.00-1.60									1.11-1.67		1.00-1.18	1.29
D$_1$H./D$_1$B.	1.04-2.58	2.30-3.00	1.22-2.09	2.00-2.58	2.18-2.80	2.50-2.80	2.58-3.00	2.66-2.94	2.04-2.73	2.52-2.75	2.12-2.42	2.40-3.00	2.10-2.42	2.43-3.00	2.43-2.63	2.33-2.66	2.10
D$_2$H./D$_2$B.	1.12-1.54	1.30-1.71	1.39-2.41	1.66-2.64	1.58-2.17	1.33-2.43	1.66-1.87	1.93-2.00	1.68-2.08	1.88-2.00	1.33-1.66	1.30-2.00	1.33-1.66	1.64-1.72	1.67-1.79	1.66-1.69	2.07
A.H./A.B.	1.18-1.47	0.93-1.48	1.09-1.69	1.33-1.82	1.29-1.75	1.20-1.53	1.36-1.67	1.92-2.00	1.60-2.08	1.50-1.62	1.39-1.72	0.95-1.10	1.39-1.82	1.50-1.55	1.55-1.61	1.32-1.64	1.66
P.H./P.B.	2.00-3.23	2.18-3.64	3.20-4.00	2.80-3.18	2.80-4.67	3.10-3.93	3.33-3.42	2.87-3.00	2.62-3.93	2.82-3.00	2.76-2.92	2.78-4.30	2.76-2.92	2.83-3.23	3.96-4.17	3.00-3.53	3.78
V.H./V.B.	1.88-4.35	2.00-2.82	2.16-2.60	1.47-2.77	2.00-2.62	2.40-2.94	2.75-3.50	1.87-2.25	2.50-3.00	2.40-2.90	1.29-1.58	1.83-2.83	1.29-1.58	2.09-2.37	2.42-2.78	2.60-2.70	2.07
P.L./Ax.Sc.	1.82-5.90	2.56-3.23	2.28-3.32						2.54-3.54					2.89-3.18	3.12-3.33	2.50-3.78	3.28
D$_1$H./D.Ob.	1.12-2.42	1.44-1.91	1.18-1.72	1.56-1.82	1.21-2.30	1.45-1.68	1.72-2.60	1.45-1.71	1.16-1.55	1.57-1.62	1.45-1.78	1.67-3.60	1.45-3.60	1.24-1.48	1.31-1.48	2.19-2.40	1.75
V.L./V.Ob.	1.70-3.11	1.33-2.50	1.44-1.82	3.00-3.82	1.75-3.00	1.54-2.76	2.75-3.80	2.10-2.57	1.56-2.00	2.23-3.00	1.58-2.82	2.75-3.87	2.58-2.82	1.35-1.90	2.48-3.00	2.36-2.55	2.38
V.L./I.V.F.	1.55-3.05	1.47-1.94	1.57-1.95	1.94-2.25	1.70-2.37	2.07-2.61	1.93-1.94	1.75-1.80	1.67-2.06	?	1.70-1.82	1.37-2.16	1.70-1.82	1.90-2.00	2.48-3.00	2.00	2.07

when the mouth is closed. The nostrils are widely apart, the anterior nearer to the upper lip than to the posterior nostril; the posterior nearer to the eye than to the anterior; the anterior nostril always below the level of the edge of the orbit; the posterior usually so but sometimes above the orbit level. Teeth absent from vomers, palatines, pterygoids, and tongue. Scales cycloid or more usually feebly ctenoid, frequently with a secondary cycloid squamation. Anal fin origin in advance of the 2nd dorsal origins. Adipose eyelid prominent. Gill membranes extending far forward, not broadly connected across the isthmus. Gut includes a gizzard. Basisphenoid, basioccipital process, and 2nd vertebral process absent; posterior opening of myodome narrow. *Arnion* Gistel and *Ello* Gistel (1848) are absolute synonyms of *Mugil.* The genus *Querimana* Jordan and Gilbert (1883) includes the young of both *Mugil* and *Myxus* in the post-larval stage with only 2 anal spines. *Oxymugil* Whitley (1948*a*) differs from typical *Mugil* species only in the broader and more elongate preorbital.

2. Genus LIZA Jordan & Swain

Liza Jordon & Swain, 1884.

Mouth terminal; lips thin, the lower projecting horizontally, but not folded downwards; the teeth are simple ciliform or setiform, in a single row in each lip, sometimes with scattered teeth behind the outer row of the upper jaw; the teeth in the lower lip are often wholly embedded in the lip in older specimens. No papillae, lamellae, or posterior folds externally; though sometimes with papillae inside the lips. A symphysial knob at the tip of the lower jaw. The preorbital is usually broad, notched, and denticulate. The maxillary is fixed anteriorly, and exposed posteriorly when the mouth is closed; maxillary and premaxillary hooked downwards. The nostrils are close together, closer than the anterior is to the upper lip or the posterior to the eye; nostrils below the level of the upper edge of the eye. Usually teeth on vomers, palatines, pterygoids, and tongue, sometimes absent from vomers and palatines. Scales cycloid or ctenoid; anal fin origin well in advance of 2nd dorsal origin. Adipose eyelid variably developed, but obsolescent in many species, being reduced to a rim about the eye. Gill membranes extend far forward, not broadly connected across isthmus. Gut includes a gizzard. A weak basisphenoid and basioccipital; 2nd vertebral process present, posterior opening of the myodome variably narrow or wide.

In Table 1 several named genera are relegated to synonyms of this genus. *Liza* was proposed as a subgenus by Jordan and Swain (1885) for mullets without an adipose eyelid. As there are all stages of obsolescence of the eyelid this criterion was never satisfactory though the name was used generically and subgenerically by several workers.

Popov (1930) proposed *Protomugil* as a subgeneric name for *Mugil saliens* Risso. Popov (1930) also extended the definition of the genus *Liza*. The modern formulation of the genus is owed to Schultz (1946) who, however, used the name *Chelon* which is valid only from the time of Jordan and Evermann (1917), Rose (1793) not having used the name binominally. Consequently *Liza* Jordan and Swain (1885) takes precedence. Schultz (1946) pointed out that *Chelon* Oshima (1922) is not used as by Jordan and Evermann, but refers to *Crenimugil* Schultz.

Gracilimugil Whitley (1941) and *Planiliza* Whitley (1945) do not show generic differences from *Liza*, the points listed by Whitley being of only specific value. *Moolgarda* Whitley (1945) is a difficult case. No type specimen was retained. Specimens in the Australian Museum and the Perth Museum labelled by this name are *Liza dussumieri* (Cuvier and Valenciennes) and do not agree with Whitley's description, though they may be the variants he mentioned as having maxillae exposed and without axillary scales. *Heteromugil* Schultz differs from *Liza* only in the possession of tricuspid instead of simple teeth. It is doubtful if one difference such as this, distinct though it is, is sufficient to be considered as generic. *Strializa* Smith (1948) varies only in the possession of scales with several mucous canals; *Pteromugil* Smith (1948) is stated to have no teeth on the palatines or vomers but a specimen of the type species kindly forwarded to the author by Professor J. L. B. Smith bore fine teeth on both.

3. Genus AGONOSTOMUS Bennett

Agonostomus Bennett, 1832.

Mouth subterminal in the young, becoming somewhat inferior in older specimens. Lips thick, lower not folded down. Teeth in a wide band on both jaws; the outer rows on both lips are simple but the inner rows of the upper lip are bifid or trifid and occasional bifid teeth occur on the lower lip. No papillae, lamellae, or posterior folds on lips. No symphysial knob on tip of lower jaw. Preorbital denticulate, but without a notch. The maxillary is fixed anteriorly, it and the premaxillary not hooked downwards posteriorly, maxillary reaches behind the preorbital and underneath the eye. The nostrils in line with the top of orbit very close together—remote from both eye and upper lip. Teeth on vomers and palatines, but not on pterygoids and tongues. Adipose eyelid absent. Scales ctenoid. Gill membranes extend far forward, not broadly connected across isthmus. Gut without a gizzard.

No specimens of this extra-Australian genus have been examined by the author, the generic definition being taken from published descriptions. Schultz (1946) described the lips as terminal. Bennett's original (1832) description stated "Rostrum subproductum, os inferum" and the type is said to differ from *Mugil* in shape and situation of the mouth. Hildebrand (1925) said that the mouth becomes more inferior with age.

Agonostomus Gunther (1861) is not equivalent to *Agonostomus* Bennett but is synonymous with *Cestraeus* Cuvier and Valenciennes as pointed out by Weber and de Beaufort (1922).

4. Genus JOTURUS Poey

Joturus Poey, 1860.

Mouth inferior, overhung by the fleshy snout which projects beyond the lips. Multicuspid teeth in a band on jaws internal to the narrow but fleshy lips. The band on the lower jaw is interrupted by a wide median gap. No papillae, lamellae. No symphysial knob on the lower jaw. The narrow preorbital neither notched nor denticulate. The maxillary and premaxillary not hooked down posteriorly. Maxillary not visible when mouth closed. The nostrils are very close together in a line with the top of the orbit, remote from snout. Teeth on vomers, palatines, and tongue, but apparently not on pterygoids. Adipose membrane absent. Scales ctenoid. Gill membranes extend far forwards somewhat broadly connected across isthmus.

This Central American genus does not occur in Australia.

5. Genus CESTRAEUS Cuvier & Valenciennes

Cestraeus Cuvier & Valenciennes, 1836.

Upper lip forms tip of snout, but mouth inferior, the lower lip fitting in behind the upper. Thick lips on both jaws, the upper not particularly deep laterally but widening medianly; externally along the lateral portions of the lower lip are strips of transverse, closely set membranous lamellae; posteriorly the mandible ends in 1 or 2 pairs of fleshy lobes which join a pair of similar lobes from the posterior of the upper lip. A row of simple teeth in both lips; those in the lower lip only medianly, and only sparse. No papillae. A low symphysial knob on the lower jaw. Preorbital broad, the posterior edge denticulated, reaching below the eye; the ventral edge without a notch and with only obsolescent denticulations. Maxilla fixed anteriorly, posteriorly it and the premaxillary are straight. Nostrils close together, level with the upper edge of the orbit, remote from the upper lip and eye. Teeth on vomers in some species, but not on palatines, pterygoids, or tongue. Adipose membrane obsolescent, not extending on to orbit. Scales ctenoid. Gill membranes extending far forward, not broadly joined across the isthmus. Gut includes a gizzard.

Schultz (1946) recorded the genus as having no symphysial knob, but specimens of *Cestraeus goldiei* Macleay and a specimen of *Cestraeus plicatilis* Cuvier and Valenciennes from New Caledonia in the Australian Museum all have a low symphysial knob. Schultz also stated that teeth were apparently absent from the vomer. This is true of *Cestraeus plicatilis* but teeth are present on the vomers in *Cestraeus goldiei.*

6. Genus CHAENOMUGIL Gill

Chaenomugil Gill, 1863.

Upper lip terminal; mouth somewhat inferior; the lower lip fitting behind the upper when the mouth is closed. Both lips thick. The lower lip is directed downwards, a band of small bifid teeth on each jaw. No fleshy lobes or lamellae posteriorly on lips; but a few rows of low papillae on the lower part of each lip. Symphysial knob undeveloped. Broad preorbital not notched; obsolescently denticulate anteriorly, more distinctly denticulate posteriorly. Maxilla and premaxilla not hooked downwards. Nostrils very close together, level with the upper edge of the orbit, remote from upper lip and eye. Adipose membrane obsolescent, not intruding upon eye. Teeth on the tongue, but not on vomers, palatines, or pterygoids. Scales ctenoid. Gill membranes extending far forward, not broadly connected across the isthmus.

This genus, which occurs in Central American waters of the Pacific Ocean, is not found in Australia.

7. Genus XENOMUGIL Schultz

Xenomugil Schultz, 1946.

Upper lip terminal, mouth somewhat inferior, lower lip fitting behind the upper when the mouth is closed. Both lips thick, the lower lip directed downwards, 1 or 2 rows of simple setiform teeth in both lips. No posterior lobes, lamellae, or papillae. A low symphysial knob. Narrow preorbitals not notched but denticulate ventrally and posteriorly. Maxilla and premaxilla not hooked downwards posteriorly. Nostrils in line with upper edge of orbit, but well separated, anterior equidistant from posterior and from upper edge of lips; posterior nostril nearer to eye than to anterior nostril. Adipose eyelid well developed. No teeth on palate or tongue. Scales cycloid. Gill membranes extending far forward, not broadly connected across the isthmus.

This genus from the Galapagos is not dissimilar to *Chaenomugil* but the differences recorded by Schultz (1946) seem sufficient to separate them. No specimens have been available to the present author.

8. Genus CRENIMUGIL Schultz

Crenimugil Schultz, 1946.

Mouth terminal. Lips thick, bearing papillae externally and internally; obsolescent on the lower lip in some species; papillae are crenulate in older specimens. The lower lip slightly folded. Lips without teeth, which seem to be represented by the papillae. Symphysial knob present. The preorbital is very broad and notched, strongly denticulate posteriorly but ventrally smooth or only obsolescently denticulate. Maxilla and premaxilla hooked downwards, but the maxilla is not exposed when the mouth is closed. Nostrils level with upper edge of the eye, the anterior equidistant from upper edge of lip and from posterior nostril, which is nearer to the eye than to the anterior nostril. Teeth on palatines and tongue but not on vomers and pterygoids. Adipose eyelids obsolescent, not intruding upon orbit. Scales cycloid. Gill membranes extending far forward, not broadly connected across the isthmus. Anal origin in advance of 2nd dorsal origin. Gut includes a gizzard. A stout basisphenoid is present, the basioccipital process is long. No 2nd vertebral process; posterior opening of the myodome wide.

Chelon of Oshima (1922) is this genus, not the *Chelon* of other authors.

9. Genus ALDRICHETTA Whitley

Aldrichetta Whitley, 1945.

Mouth terminal, lips not thick, the lower not folded down, without papillae, lamellae, or posterior lobes. Bands of minute setiform teeth on both jaws. A symphysial knob present. The preorbital is narrow, notched, and denticulate. The maxillary is fixed anteriorly. Posteriorly the maxillary and premaxillary are not hooked downwards. Large nostrils closer together than to upper lip or to eye. Adipose eyelid obsolescent, not intruding upon eye. Sharp-pointed teeth plentifully supplied on vomers, palatines, pterygoids, and the tongue, on the pharyngeal "cushions" and gullet floor; more numerous in older fish. Scales cycloid. Gill membrane extending far forward, not united broadly across the isthmus. Anal origin well in advance of 2nd dorsal origin. Gut includes a gizzard. A weak basisphenoid and small basioccipital process present. Second vertebral process absent. Posterior opening of myodome narrow.

The sole species of this genus, *A. forsteri* (Cuvier & Valenciennes) has usually been assigned to *Agonostomus*. But despite the superficial similarities such as the abundant teeth, this Australian estuarine species has no real relationship with the American freshwater genus. One major anatomical difference is the presence of a definite gizzard in *Aldrichetta*, whereas *Agonostomus* is without this feature. *Aldrichetta* has cycloid scales, whereas those of *Agonostomus* are ctenoid. The lips of *Aldrichetta* can by no means be called thick. They are much thinner than those of *Mugil cephalus*, the type species of *Mugil*, which is agreed to have thin or only moderately thick lips. The presence of a symphysial knob also seems to distinguish *Aldrichetta* from *Agonostomus*. *Agonostomus* is reported to have no teeth on the tongue, whereas *Aldrichetta* has the tongue almost entirely covered by teeth in old specimens.

10. Genus TRACHYSTOMA Ogilby

Trachystoma Ogilby, 1887.

Mouth terminal, lips thin, a single row of ciliform teeth in both jaws tending to become embedded in the lips and hidden in adults, particularly in the lower jaw. No papillae, lamellae, or posterior folds on lips. Lower lip not folded down. A symphysial knob present. The denticulate preorbital is broad; a feeble notch in young fish, becoming obliterated in older specimens. Anterior nostrils closer to posterior than to upper lip; posterior nostril equidistant from anterior nostril and eye; maxillary fixed anteriorly; it and the premaxillary are not hooked downwards posteriorly; and maxilla not exposed when mouth closed. Teeth on vomers, palatines, and pterygoids. Only a few small patches of teeth on tongue. Adipose eyelids obsolescent, intruding only slightly on orbit. Scales cycloid, sometimes ctenoid on belly. Anal fin origin in advance of the 2nd dorsal origin. Gut includes a gizzard. Gill membranes extending far forward, not broadly joined across the isthmus.

In many respects *Aldrichetta* is similar to *Trachystoma,* but the teeth are far more abundant in the former genus and spread to the gullet. However, they are very similar in general characters and may represent only the extremes of development of a genus; *Trachystoma* with feeble teeth and *Aldrichetta* with unusually well-developed teeth for a mullet.

11. Genus MYXUS Gunther

Myxus Gunther, 1861.

Mouth terminal; lips thin, a single row of closely set incisor-like teeth in both jaws. No papillae, lamellae, or posterior folds on lips. Lower lip not folded down, a symphysial knob present. Preorbital wide, denticulate, not notched, reaching ½ way under eye. Nostrils close together at level of upper edge of orbit, the adipose membrane only feebly represented, not intruding upon orbit. Teeth on vomers and palatines but not on pterygoids or tongue. Maxilla and premaxilla not hooked down; maxilla, which is firmly fixed anteriorly, is not exposed posteriorly when the mouth is closed. Scales cycloid. Anal fin origin in advance of 2nd dorsal origin. Gut includes a gizzard. Gill membranes extending far forward, not broadly connected across the isthmus.

Schultz (1946) says "teeth . . . . . . probably on tongue"; but this organ seems to be toothless.

12. Genus VALAMUGIL Smith

Valamugil Smith, 1948.

Mouth terminal, lips thin, ciliform teeth in a single sparse scattered row in both jaws. No papillae, lamellae, or posterior lobes. Lower lip not folded down. A symphysial knob present; denticulate. Preorbital moderate, weakly notched. Nostrils apart — nearer to the lip and the eye than to each other. Adipose membrane variably developed. Teeth on pterygoids and tongue but not on vomers and palatine. Premaxilla straight, but maxilla bent down slightly posteriorly. Maxilla hidden when mouth closed. Scales cycloid. Anal fin origin opposite that of 2nd dorsal origin. Gut includes a gizzard. Gill membranes extend far forward, not broadly connected across the isthmus. Pectoral fins unusually long.

This is an Indo-Pacific genus.

13. Genus RHINOMUGIL Gill

Rhinomugil Gill, 1863.

Snout produced over the lips, mouth inferior. Lips thin; ciliform teeth in a single row in both. No papillae; lamellae, or posterior lobes. Lower lip not folded down. A symphysial knob present. Narrow preorbital comes almost to a point posteriorly, not notched, and only a few prominent denticulations. Nostrils well apart. Posterior opposite the upper edge of the orbit, the anterior 2/3 of way down eye. Eyes small, almost on top of head; interorbital concave, adipose eyelid obsolescent. No teeth on palatines or tongue. Maxilla fixed, mouth not protrusible; maxilla and premaxilla not hooked downwards, and maxilla hidden. Scales ctenoid. Anal fin origin well in advance of 2nd dorsal origin. Gill membranes extend far forward, not broadly joined across the isthmus.

IV. Description of Species

Details of proportional measurements will be found in Table 3.

Key to Australian Species of the Genus Mugil

Lateral scales 38-42; 8 anal rays	*M. cephalus*
Lateral scales 31-32; 9 anal rays	*M. georgii*

Key to Australian Species of the Genus liza

1.	Lateral scales 25-27	*L. vaigiensis*
	Lateral scales more than 28	2
2(1).	Anal rays 11	*L. ramsayi*
	Anal rays 10	*L. argentea*
	Anal rays 9	3
3(2).	Tongue notched anteriorly	*L. diadema*
	Tongue not notched	4
4(3).	Adipose eyelid well developed	*L. strongylocephalus*
	Adipose eyelid obsolescent	*L. dussumieri*

Key to Australian Species of the Genus Valamugil

Lateral scales 37-92	*V. seheli*
Lateral scales fewer than 37	*V. buchanani*

Key to Australian Species of the Genus Crenimugil

Lateral scales 38-42. Transverse scales 13-14	*C. crenilabis*
Lateral scales 33-35. Transverse scales 11-12	*C. labiosus*

The other genera have only one species in Australasian waters.

1. MUGIL CEPHALUS Linnaeus

Plate 1, Fig. 1

Mugil cephalus Linnaeus, 1758, p. 316 (European seas); McCulloch, 1921*a*, p. 48; 1922, p. 38; 1927, p. 39 (N.S.W.); 1929, p. 114 (Australia); 1934, p. 38 (N.S.W.); Waite, 1923, p. 107; 1925, p. 230; 1928, p. 6 (S.A.); Phillipps, 1927*a*, p. 30; 1927*b*, p. 12 (N.Z.).

Mugil dobula Gunther, 1861, p. 420; (Perth, W.A., Aneitum); 1877, p. 214, pl. 120, fig. A (China); 1880, p. 61 (Hilo, Hawaii); Kner, 1865, p. 224 (Hong Kong); Bleeker, 1873, p. 143 (China); Macleay, 1878, p. 364 (Darwin); 1880, p. 414 (Australia); 1881, p. 47 (Australia); 1884*b*, p. 208 (Burdekin and Mary R.); Castelnau, 1879*a*, p. 50 (Norman R., Queensland); 1879*b*, p. 353 (Port Jackson); Ogilby, 1887, p. 27 (N.S.W.); 1893, p. 109 (N.S.W.); Saville-Kent, 1893, p. 294 (Moreton Bay to Cooktown); Steindachner, 1900, p. 501 (Honolulu); Dannevig, 1902, p. 50; Waite, 1904, p. 22 (N.S.W.); 1921, p. 83 (S.A.); Stead, 1906*a*, p. 75, fig. 27 (Australia); 1908, p. 40; Roughley, 1916, p. 37 (N.S.W.); Chu, 1931, p. 104 (Hong Kong); Whitley, 1948*a*, p. 17 (W.A.).

Mugil occidentalis Castelnau, 1873, p. 135 (Port Phillip); Macleay, 1885, p. 41 (Manning R.).

Mugil gelatinosus Klunzinger, 1879, p. 395; Macleay, 1885, p. 41 (Murray R., S.A.).

Mugil mulleri Klunzinger, 1879, p. 395; Macleay, 1885, p. 42; McCulloch, 1929, p. 116 (King George's Sound); Whitley, 1948*a*, p. 17 (W.A.).

Mugil grandis Castelnau, 1875, p. 32 (N.S.W.); 1879*b*; p. 353 (Port Jackson); Macleay, 1880, p. 412 (N.S.W.); 1881, p. 47 (Brisbane and N.S.W.); Tenison-Woods, 1882, p. 71, pl. 30; Ogilby, 1887, p. 27 (N.S.W.).

Mugil marginalis De Vis, 1885, p. 870; McCulloch, 1929, p. 114; McCulloch and Whitley, 1925, p. 141 (Brisbane).

Mugil marginatus Saville-Kent, 1893, p. 294 (Barrier Reef).

Mugil perusii Hutton, 1872*a*, p. 36, 113, pl. 6, fig. 57 (N.Z.); Thomson, 1892, p. 211 (N.Z.) (? non Cuvier and Valenciennes 1836).

Mugil hypselosoma Ogilby, 1897*b*, p. 74 (Tas.).

Mugil oeur Ogilby, 1897, p. 74 (Moreton Bay); Tosh, 1903, p. 3 (Moreton Bay). (For a fuller synonymy of extra-Australian records see Jordan and Swain, 1885, p. 261; Weber and de Beaufort, 1922, p. 238; Fowler, 1928, p. 125.

Type locality: European seas. No type specimen.

Vernacular names: Sea mullet, bully mullet, mangrove mullet. Hard-gut mullet (N.S.W., Queensland), sand mullet, poddy (Vic.), mullet (S.A.), river mullet or sea mullet, bully mullet (W.A.).

D. IV, I, 8; A. III, 8; V I, 5; P. 16-17; C. 18-20. The pectoral fin rarely has 17 rays and the querimana stage has only 2 anal spines and 9 anal rays.

Scalation.—L. 1 38-42 + 3-5; tr. 14-15; predorsal 24-26; cheek-scales 3-4 rows. The scales are cycloid in the young, feebly ctenoid in older fish; posterior border slightly scalloped with a central emargination; marked by a regular series of circuli and annuli; a single somewhat oblique mucous groove on some scales. A secondary squamation of small cycloid scales is developed over much of the integument.

Body robust, head markedly broad, its length greater than the body depth, snout length greater than the diameter of eye, its anterior profile sharply curved, the moderately broad upper lip being almost vertical; mouth terminal cleft oblique, not quite ½ as deep as broad; lower lip wafer-thin with a feebly double symphysial knob; both lips with a row of simple setiform teeth along the edge, usually in a single row, but sometimes with a few scattered teeth behind the outer row; teeth may be lost or covered by lip tissue in older specimens. No teeth on the palate. The end of the maxilla is concealed when the mouth is closed, sometimes it is visible as a thin streak above the lip. The lower jaw outline is somewhat angular centrally, rounded laterally; the mandibulary angle acute in young specimens, obtuse in most specimens over 35 cm long. Nostrils equidistant from each other and from the upper lip and orbit in young but in older fish the anterior nostril is nearer the edge of the upper lip than it is to the posterior nostril and the latter is nearer the orbit. The anterior nostril is below the level of the eye, the posterior above it; a prominent adipose eyelid almost obscures the eye, leaving only a narrow slit over the pupil; it covers a large portion of the head, obscuring the preorbital and posteriorly running twice as far as it covers anteriorly. Interorbital very broad. Intergular usually lanceolate; margin of opercle at pectoral base level almost vertical with a slight backward projection over the base of the pectoral; the preorbital is not notched, with only a moderate posterior border, bearing 6 denticulations; the anterior border with about 14.

The pectoral fin reaches the 10th scale of postopercular series but not to the origin of the 1st dorsal fin and turned forward reaches to eye, but not to pupil; it has a distinct axillary scale; the ventral fins relatively short, arising under the posterior 1/3 of the pectoral and reach the level of the origin of the 1st dorsal. The 1st dorsal origin is nearer the snout than the caudal base and is at the 12th scale and that of the 2nd dorsal at the 24th. The 2nd dorsal is slightly higher than the 1st dorsal; but is not as high as the anal fin whose origin is well in front of that of the 2nd dorsal. The 2nd dorsal and the anal fins have minute scales on their anterior thirds and are obscurely concave in outline. Interventral flange longer than ventral obbasal. The bases of all fins relatively short. The obbasal scales are large. The caudal fin deeply forked.

Gill rakers 24-36/50-76, the number increasing with age; pyloric caecae 2.

Size.—Attains 570 mm L.C.F. and a weight of 7½ lb. Growth rate approximates to 14, 24, 33, 40, 46, 50, 55 cm for 1st, 2nd, etc. years.

Coloration.—The colour varies according to habitat; mullet from the sea are olive-green dorsally with bright silvery sides, shading into off-white below; those taken from the rivers are very dark dorsally, having the clear olive-green obscured by a suffusion of a deep blue to dirty brown color, the sides are less silvery and are dull. The 6 or 7 median lateral rows of scales bear not very prominent longitudinal brown bands produced by groups of small brown pigment spots in the centre of the scales. The fins are minutely dotted with black, producing a dusky appearance, except for the ventrals, which are a pale yellowish colour. Around the iris there is a golden ring which gradually fades in preserved material. A dark blue or violet spot at the base of the pectoral fin becomes black on preservation.

Discussion.—Australian specimens of *Mugil dobula* agree in all essentials with specimens of *Mugil cephalus* from the Adriatic Sea, from the Mediterranean near Monaco, from South Africa, and from Japan which have been studied by the author. Smith (1935) stated that American examples of the species are identical with the South African. According to Jordan and Swain (1885), records of *Mugil cephalotus* in the American area refer to *Mugil cephalus,* and Weber and de Beaufort (1922) agreed that records from the East Indies also refer to *Mugil cephalus;* but both Jordan and Swain (1885) and Fowler (1935) agreed that the original *Mugil cephalotus* of Cuvier and Valenciennes is a valid species though Weber and de Beaufort considered it to be synonymous with *cephalus.* The original description is too incomplete for any sure decision to be made. The idea that the large silvery Australian sea mullet was a distinct species from the smaller dark-backed river mullet was held by several earlier authorities who distinguished the large form as *Mugil grandis.* Dannevig (1902) cast doubt on this idea on morphological grounds, and the matter was proved beyond doubt by tagging experiments reported by Kesteven (1942). *Mugil marginalis* De Vis is *cephalus. Mugil hypselosoma* Ogilby is an unusually deep specimen of the species. *Mugil perusii* Hutton (1872*a,* 1872*b*) and Thomson (1892) from New Zealand, and *Mugil oeur* Ogilby (1897*a*) and Tosh (1903), as well as *Mugil occidentalis* Castelnau (1873), *M. gelatinosus* Klunzinger (1879), and *M. mulleri* Klunzinger (1879) do not differ in description from *cephalus,* being within the range of differences associated with growth.

Material.—Australian Museum: B3869, B3870 (Tirano, Adriatic); IB2836 (New Caledonia); IA2678-9 (Hawaii). Queensland Museum: 1 3631-9, 1 1893, 1 3888 (unlocalized). Museum of Zoology Department, University of Tokyo: 6934 (Bonin Is.); 21950 (Kagoshima) 28614-5, 28618 (Tanagoshima). C.S.I.R.O. Cronulla Laboratory: Greenough R., W.A., 8 specimens 12.3-15.8 cm; Chapman R., W.A., 2 specimens 11.2 and 14.7 cm; Swan R., W.A., 17 specimens 8-21.0 cm; Tweed R., N.S.W., 61 specimens 3.1-13.8 cm; L. Illawarra, 36 specimens 8.0-10.5 cm. Other material: Obizu R., Irawaka R. (Japan); Knysna (South Africa); Monaco. Numerous specimens from Shark Bay, Abrolhos Is., and all the Western Australian rivers between the Murchison R. and Cordinup R. (east of Albany); the mouth of the Murray R., S.A.; Lakes Entrance, Vic.; and all the rivers from Eden to Rockhampton along the eastern Australian coast.

2. MUGIL GEORGII Ogilby

Plate 1, Fig. 2

Mugil georgii Ogilby, 1897*b*, p. 77 (Georges R.); Tosh, 1903, p. 7 (Moreton Bay); Waite, 1904, p. 22 (Georges R.); Stead, 1908, p. 43 (N.S.W.); Cockerell, 1913, p. 53 (Queensland); McCulloch, 1921*a*, p. 48 (N.S.W.); 1921*b*, p. 129, pl. 22, fig. 1 (Port Hacking, Karuah R., Brisbane R.); 1922, p. 38 (N.S.W.); 1927, p. 38 (N.S.W.); 1929, p. 114 (N.S.W., Queensland); 1934, p. 38, fig. 139*b* (N.S.W.); McCulloch and Whitley, 1925, p. 141 (Moreton Bay, Brisbane R.).
Mugil nortoni Ogilby, 1908, p. 22 (Brisbane R.).

Type locality: Georges River, N.S.W. Holotype 14936 Australian Museum.

Vernacular names: fan-tail mullet, silver mullet.

D IV, I, 8; A.III, 9; V.I, 5; P.15; C.14 (+7).

Scalation.—L.1, 31-32 tr. 12-13; predorsal 20-21; cheek scales 3-4 rows scales cycloid dorsally and laterally ctenoid on belly, gently scalloped along posterior border with about 7 radii, arranged in a fan-like manner, mucous groove small, central, and running along the antero-posterior axis.

Body deep, robust, upper profile of head convex; its length less than body depth; snout shorter than diameter of eye; upper lip moderate, almost vertical; mouth terminal, cleft nearly horizontal; a little less than ½ as deep as broad; lower lip wafer-thin; symphysial knob double; upper lip bears a row of fine ciliate teeth; lower lip edentate; palate toothless; maxillae concealed when mouth is closed; outline of lower jaw angular; mandibulary angle obtuse. Nostrils nearer to the edge of the upper lip and to eye than to each other; anterior nostril below the upper edge of the eye; posterior nostril above it; a prominent adipose eyelid obscures about ½ the iris anteriorly and ⅓ posteriorly but reaches the pupil only in very large specimens. Posteriorly the adipose tissue reaches about ⅔ of the head length; but anteriorly it forms only a small triangle scarcely reaching the posterior nostril. Interorbital of only moderate width; margin of the operculum at pectoral base level inclined posteriorly, with a slight dorsal fold which does not reach over the pectoral base. The preorbital is almost quadrangular; without a notch; the posterior border being only moderate in width though with denticulations (about 15); the anterior border has obsolescent denticles (3-6 in number) which do not project forward, but downward inside the edge of the bone.

The pectoral fin only reaches the 10th scale; not nearly to the origin of the 1st dorsal fin; turned forward it just reaches to the front of the eye; it has a marked axillary scale. The ventral fins are about ½ way along the pectoral length and reach the level of the base of the 2nd dorsal spine of the 1st dorsal fin. The 1st dorsal origin, at the 13th scale, is distinctly nearer to the caudal base than to the snout. The 2nd dorsal origin, at the 23rd scale, is about ½ way along the anal fin; it is distinctly higher than the relatively low 1st dorsal, but is a little lower than the anal height. The pectoral and caudal bases scaly; the anal scaly basally, and the 2nd dorsal very slightly scaled anteriorly. Obbasal scales are relatively short; the interventral flange shorter than the ventral obbasal. Second dorsal and anal fins only moderately concave; caudal broadly concave, not deeply forked.

Gill rakers 20/56; pyloric caecae 22.

Size.—The largest specimen seen by the author was 25.4 cm L.C.F. and weighed 13.0 g.

Coloration.—Greenish brown above; silver sides shading into off-white below; fins pale, 2nd dorsal, anal, and caudal with dusky borders; membrane of the 2nd dorsal speckled with dark brown pigment spots; a deep purple axillary spot at the upper base of the pectoral; a golden segment over the upper ⅓ of the iris; and a much smaller gold segment (not as wide as the pupil) ventrally.

Discussion.—McCulloch (1929) has dealt with the identity of *Mugil nortonis* Ogilby with this species. McCulloch (1921*b*) stated that there are 13 pyloric caecae. Directly visible on inspection of the gut are 14 caecae; but there are 8 others hidden by the lobes of the liver.

This species may be confused with *Mugil cephalus* owing to the marked adipose eyelid, but the number of lateral scales and of anal rays and pyloric caecae readily distinguish the species.

Material.—Australian Museum: I 4936 (Georges R., holotype); I 12843-4; I 14949-56 (Port Hacking); I 12845 (Karuah, Port Stephens). Queensland Museum: I 1116 (Nerang R.); I 1312-4 (Moreton Bay); I 3104 (Indooroopilly, Brisbane R.); I 1697 (Breakfast Creek, Brisbane R.). C.S.I.R.O. Laboratory, Cronulla: Tweed R. (6 spec.), Moreton Bay (5 spec.), Hawkesbury R. (1 spec.), Port Macquarie (1 spec.). Other material: Numerous specimens from Tweed R., Moreton Bay; Bribie Passage; Noosa R., Maroochy R., Burnett R.

3. LIZA STRONGYLOCEPHALUS (Richardson)

Fig. 6

Mugil strongylocephalus Richardson, 1846*a*, p. 249 (fig.) (Hong Kong; Sea of China); Gunther, 1861, p. 425, fig. 3 (China); Bleeker, 1873, p. 143 (China); Sauvage, 1881, p. 106 (Swatow); Rutter, 1897, p. 70 (China); Chu, 1931, p. 104 (China); ? Reeves, 1927, p. 8 (China); Fowler, 1935, p. 139 (Hong Kong); Smith, 1935 p. 606, fig. 8 (Durban, Isipingo Lagoon, Beira, Bay of Bengal); 1948, p. 836 (tropical Indo-Pacific); 1949, p. 317, fig. 877 (Indo-Pacific).

Mugil cunnesius Bleeker, 1852, p. 454 (Borneo); 1858, p. 279 (Indonesian Archipelago); 1860*a*, p. 8 (Sumatra); Day, 1878 p. 349; pl. 74, fig. 3 (Bay of Bengal); Waite, 1904, p. 22 (Port Jackson (error!))? (non Cuvier and Valenciennes 1836).

Mugil engeli Day, 1865, p. 139 (Malabar) (non Bleeker 1854).

Mugil longimanus Gunther, 1861, p. 428 (East Indies); 1877, p. 215 (South Seas); Steindachner, 1879, p. 5 (Cleveland Bay); Klunzinger, 1879, p. 395 (Cleveland Bay); Macleay, 1884*b*, p. 41 (Cleveland Bay); Ogilby, 1887, p. 27 (Port Jackson (error)); 1908, p. 41 (Queensland); Saville-Kent, 1886, p. 370 (Queensland); 1893, pp. 294, 370 (Great Barrier Reef); Seale, 1914, p. 61 (Hong Kong); McCulloch, 1921*b*, p. 130; (Cleveland Bay, Philippines, Bombay); 1929, p. 115 (Queensland); McCulloch and Whitley, 1925, p. 141 (Cleveland Bay); Paradice and Whitley, 1927, p. 81 (Northern Territory); Fowler, 1925*a*, p. 208 (South Africa); 1925*b*, p. 9 (tropical Pacific); 1928, p. 123 (Oceania); 1934, p. 308 (Oceania); 1935, p. 140 (Hong Kong); Weber and de Beaufort, 1922, p. 239 (Singapore; Sumatra; Java; Celebes; Moluccas); Chu, 1931, p. 104 (China); Herre, 1931, p. 12 (Solomon Is.).

Type locality: Hong Kong (type specimen—British Museum).

D IV, I, 8; A.III, 9; P.16.

Scalation.—L 1.33-35 tr. 11-12; 3 or 4 cheek scales; 18 or 19 predorsal. Scales cycloid, with a broad membranous edge; 4 or 5 radii, a straight elongate narrow mucous canal, a secondary squamation evident over nuchal region.

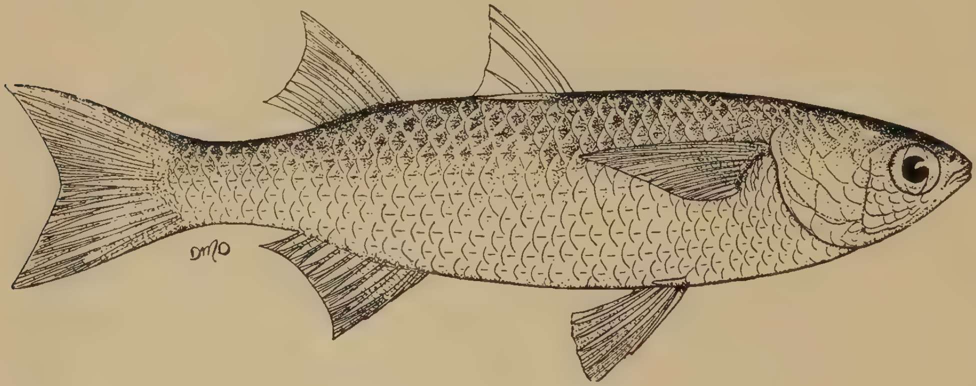

Fig. 6.—*Liza strongylocephalus* (after Smith 1949).

Body robust, dorsal and ventral profiles convex, head length less than or equal to depth. Eye diameter greater than snout length; upper lip moderately thick; mouth terminal, mouth cleft oblique; lower lip thin with a double symphysial knob. A single row of minute ciliate teeth on upper lip; lower jaw edentate; teeth on pterygoids and tongue, but not on vomers and palatine. Posterior end of maxilla usually but not always visible when the mouth is closed; its posterior end hooked downwards. Outline of the jaw somewhat angular; mandibulary angle rectangular to obtuse. Posterior nostril nearer to edge of eye than to the anterior nostril which is equidistant from the posterior nostril and the edge of the upper lip. The adipose eyelid well developed, reaching the pupil anteriorly and posteriorly. Head width and interorbital width relatively great. Margin of the operculum at the level of the pectoral base almost vertical, with a backward projection over the base of the pectoral. Preorbital slightly emarginate but not notched; the hind end narrow.

The pectoral fin reaches the 12th to 15th scale behind the origin of the dorsal fin and turned forward reaches in front of the eye almost to the tip of the snout. There is a large axillary scale. The ventrals rather long, with long obbasal scales, which are larger than the interventral flange. The 1st dorsal fin originates at the 12th to 14th scale, nearer to snout than to caudal base. The dorsal obbasal is long, reaching almost to the posterior margin of the fin membrane. The 2nd dorsal origin is at the 20th to 22nd scale, behind the origin of the anal fin, which is falcate and higher than the 2nd dorsal, which is higher than the 1st dorsal; the anal and 2nd dorsal well covered by scales. The caudal moderately forked.

Coloration.—Silvery, greenish above; caudal with dusky margin; black axillary scale.

Discussion.—This is the Pacific species generally referred to *longimanus* Gunther. Smith (1935) is followed in making *longimanus* a synonym of *strongylocephalus.* Neither Richardson's nor Gunther's descriptions are very helpful, but there are no differences of taxonomic value. Fowler's (1935) descriptions of the 2 species differ only in some of the relative measurements, notably the length of the head and of the pectoral fin, all of which alter with age and growth. Day's (1865) description of *engeli* from Malabar is in accord with this species but differs from *engeli* as described by Bleeker (1854). The erroneous locality record of "Port Jackson" arose from a mis-report in the Zoological Record as explained by McCulloch (1921*b*). *Mugil cunnesius* of the authors listed appears to be this species, but *cunnesius* Cuvier and Valenciennes is separate, having 42-43 scales, adipose eyelid marked only posteriorly, snout equal to eye diameter, maxillary slightly visible, preorbital non-denticulate. Smith (1948, 1949) allotted this species to the genus *Mugil.* But, despite the well-developed adipose eyelid, it has teeth on pterygoids and tongue, and the maxilla is exposed; all features typical of *Liza.*

Material.—Australian Museum: IA 1614, IA 2557 (Pellier Is., Gulf of Carpentaria); IA 7682-4 (Northern Territory); IA 3067 (Adam Bay, Northern Territory); B 8069 (Bombay). South Africa: one specimen from Isipingo.

4. LIZA DUSSUMIERI (Cuvier & Valenciennes)

Plate 1, Fig. 3

Mugil dussumieri Cuvier & Valenciennes, 1836, p. 147 (Bombay; Coramandel); Bleeker, 1848, p. 637 (Indonesia); 1860*a*, p. 33 (Borneo); Day, 1870; p. 352, pl. 74, fig. 4 (India); (?) Stead, 1906*a*, p. 60; 1906*b*, p. 7; 1908, p. 42 (Clarence

R.); Weber, 1908, p. 243; 1913, p. 569 (New Guinea); ? McCulloch, 1921*b*, p. 48; 1927, p. 38 (N.S.W.); 1929, p. 115 (N.S.W., Queensland); 1934, p. 38 (N.S.W.); McCulloch and Whitley, 1925, p. 141 (Gold I., Rockhampton Bay, Queensland); Weber and de Beaufort, 1922, p. 235 (Indo-Australian Archipelago); Fowler, 1925*b*, p. 7 (Guam); 1928, p. 122 (New Guinea; East Indies; India; Australia); 1934, p. 398 (Ellice Is.); 1935, p. 142, fig. 55 (Hong Kong); Roxas, 1934, p. 401 (Philippines); Blegvad, 1944, p. 183 (Bushire Harbour; Bender Shalipur).

Mugil sundanensis Bleeker, 1853, p. 245; Macleay, 1882, p. 362 (New Guinea).

?*Mugil compressus* Gunther, 1861, p. 451; 1880, p. 68; 1881, p. 217, pl. 123, fig. *A* (N.S.W.); Castelnau, 1879*a*, p. 50 (Norman R., Queensland); Klunzinger, 1879, p. 395 (Darwin and Queensland); Macleay, 1880, p. 421; 1882, p. 48 (N.S.W.); 1884*c*, p. 269 (Normanby, Queensland); Ogilby, 1887, p. 27 (N.S.W.); Waite, 1904, p. 22 (N.S.W.); McCulloch, 1921*b*, p. 48; 1922, p. 38; 1927, p. 38; 1934, p. 38, fig. 139 (N.S.W.); McCulloch and Whitley, 1925, p. 141 (N.S.W., Queensland).

Liza compressa Jordan and Seale, 1906, p. 218 (Samoa); Kendall and Goldsborough, 1911, p. 256 (Oceania); McCulloch, 1929, p. 114 (Australia).

Mugil stevensi Ogilby, 1908, p. 17 (Gold I.; Rockingham Bay, Queensland).

Mugil tadopsis Ogilby, 1908, p. 27 (Moreton Bay); McCulloch, 1921*b*, p. 127, pl. 22, fig. 2; 1929, p. 126; McCulloch and Whitley, 1925, p. 141 (Moreton Bay; Burdekin R.; Endeavour R.).

(?) *Moolgarda pura* (partim) Whitley, 1945, p. 15, fig. 8 (Pt. Cloates, Shark Bay, Onslow, Broome); 1949, p. 342 (New Guinea); 1948*b*, p. 17 (W.A.).

Type locality: Bombay; Coramandel.

Vernacular names: green-backed mullet, brown-back mullet, brown-banded mullet.

D. IV, I, 8-9; A. III, 9; P.15.

Scalation.—L1, 28-32; tr. 10-13; predorsal 19-21; cheek-scales 3-4; scales ctenoid; with a small oblique mucous groove; about 9 radii.

Body robust; deep; dorsal profile almost straight, head length equal to body depth; snout shorter than eye length; upper lip moderate, mouth terminal, cleft slightly oblique; lower lip thin with a weakly double symphysial knob, both jaws bear very fine cilia which are more numerous in smaller specimens and almost absent in large; teeth on the pterygoids and ridged tongue but not on the vomers and palatines. Maxillae turned down and visible when the mouth is closed; outline of the jaw rounded; mandibulary angle obtuse; nostrils nearer to each other than to the eye or upper lip, posterior nostril a lunate slit, above eye; anterior just below the upper edge, circular outline; a slight adipose eyelid fails to reach the pupil, and reaches as far as the anterior nostril in front and an equal distance behind. Interorbital distance only moderate. Margin of the operculum opposite the pectoral base almost vertical. The preorbital is broad and strongly serrated; only very slightly notched.

The pectoral fin reaches the 7th or 8th scale, about 2 scales in front of the 1st dorsal origin; turned forward it reaches past posterior edge of the eye to the posterior edge of the adipose eyelid; no axillary scale. The ventral fin originates a little more than ½ way along the pectoral and reaches to level of the base of the 3rd spine of the 1st dorsal; the obbasal spine and interventral flange are of moderate length. The 1st dorsal fin origin is at the 9th or 10th scale; midway between snout and caudal base or slightly nearer latter. The 2nd dorsal arises at the 19th or 20th scale about ½ way along the anal fin, it is higher than the 1st dorsal which is equal in height to the anal; 2nd dorsal and anal fins scaly, emarginate; caudal only slightly emarginate.

Gill-rakers: 28/68, largest gill filament 3.5 times length of longest gill-raker; pyloric caecae 5.

Size.—Recorded up to about 36 cm L.C.F.

Coloration.—Greyish green postero-dorsally, brownish over head, silvery laterally shading to white below, about 5 faint stripes along upper rows of scales; dorsal fins greyish, ventrals off-white; caudal dark bluish black marginally; pectorals yellowish with a blue axillary spot. A slight gold segment on the upper part of the iris.

Discussion.—The original description of Cuvier and Valenciennes is not entirely adequate and could apply to this or 2 or 3 other species of the Indo-Pacific. The present species is certainly the *Mugil dussumieri* of Day (1878) and subsequent authors.

The *Mugil dussumieri* described as "the New Hebrides form" by Whitley (1941) is not this species, as comparison of the New Hebrides forms in the Australian Museum compared with specimens of *dussumieri* from India and elsewhere clearly shows. These New Hebrides forms have teeth on the vomer and palatines and have an axillary scale; the adipose eyelid is less well developed.

McCulloch (1921*b*) demonstrated the identity of *Mugil stevensi* Ogilby (1908) with this species.

Mugil compressus Gunther has usually been regarded as a separate species, but nothing exists in published descriptions to distinguish it from the present species except Gunther's statement that it has no adipose eyelid; and although it has been recorded as an eastern Australian species; no specimens in the Australian or Queensland Museums can be distinguished separately from *dussumieri*.

The position of *Moolgarda pura* Whitley (1945) is difficult. No type specimen was preserved. Named specimens in the Australian Museum collection do not agree with the original description; but as noted above agree with *Liza dussumieri*. The type description of *pura* states that an axillary scale exists, the maxilla is hidden, the 2nd dorsal origin is opposite the anal origin, and 36 lateral scales and 18 transverse are present. Whitley states that in cotypes "the maxilla may be exposed, the axillary scale may be absent, the anal origin a little in advance of the second dorsal origin; transverse scales numbered from 29 to 35; second transverse from 11 to 15". Although variation in such factors is usual, the range seems excessive for 1 species. Although axillary scales may be missing from specimens of a species normally bearing them, it would be straining credulity to believe that this had occurred in all the specimens listed below. The relative position of the 2nd dorsal origin is usually constant in a species. Although the tip of the maxilla may occasionally be exposed in species where it is normally hidden, the exposure of a large portion of the hind end, such as these specimens exhibit, is not normal. The specimens showing these characteristics also have fewer lateral and transverse rows of scales. While it is believed that the type described for *Moolgarda pura* is not *dussumieri,* at least some of the cotypes appear to be.

Material.—Australian Museum: B 7975 (Madras); IA 4706 (Ellice Is.); A12631-2 (New Guinea); I 9183 (Normanby I.); I 12900; I 12901; I 13225 (Shark Bay); IB 797 (Broome); IB 2335 (Port Glasgow, Papua); A 13623, A 13675 (Burdekin R.); I 14494-6 (Cooktown). Queensland Museum: I 776 (Gold I., Rockingham Bay); I 5620; I 6005 (Moreton Bay). Other material: Specimens from Shark Bay; Exmouth Gulf, Onslow. *Mugil tadopsis* Ogilby shows no differences from *dussumieri.*

5. Liza argentea (Quoy & Gaimard)

Fig. 7

Mugil argentea Quoy and Gaimard, 1825, p. 238, pl. 59, fig. 3 (Port Jackson); Schmeltz, 1866, p. 10; 1869, p. 10; 1869, p. 21 (East Indies); Macleay, 1880, p. 417 (Fitzroy R., Queensland); 1881, p. 47 (Rockhampton); Ogilby, 1887, p. 27 (N.S.W.); Tosh, 1903, p. 2, pl. 1, fig. 2 (Moreton Bay); Waite, 1921, p. 82, fig. 124 (S.A.); 1923, p. 107 (S.A.); 1928, p. 6 (S.A.); McCulloch, 1921*a*, p. 49 (N.S.W.); 1921*b*, p. 131 (N.S.W.); 1922, p. 39 (N.S.W.); 1934, p. 3*a*, pl. 4, fig. 139*f*; McCulloch and Whitley, 1925, p. 141. (Non Gunther, 1861, 1877; Jordan and Seale, 1906; Fowler, 1928, 1931.)

Mugil peronii Cuvier and Valenciennes, 1836, p. 138 (Western Port; NW. Australia); Gunther, 1861, p. 452 (NW. Australia); Castelnau, 1873, p. 151 (Vic.); 1879*a*, p. 353 (Port Jackson); Macleay, 1878, p. 360 (Port Darwin); 1880, p. 421 (Australia); 1884*b*, p. 47 (northern Australia); Ogilby, 1887, p. 27 (N.S.W.); 1893, p. 130 (N.S.W.); Waite, 1904, p. 22 (N.S.W.); Stead, 1908, p. 42, pl. 13 (N.S.W.); Roughley, 1916, p. 41, pl. 8 (N.S.W.); Fowler, 1931, p. 324 (NW. Australia; Tonga Is.).

Mugil ferrandi Cuvier and Valenciennes, 1836, p. 142.

? *Mugil convexus* De Vis, 1885, p. 868 (Cardwell, Queensland); McCulloch, 1929, p. 114 (Queensland); McCulloch and Whitley, 1925 p. 141 (Cardwell, Queensland).

Liza argentea McCulloch, 1929, p. 116 (Australia).

Type locality: Port Jackson.

Vernacular names: tiger mullet (Queensland), flat-tail, fan-tail (N.S.W., Vic., S.A., W.A.).

D.IV, I, 9; A.III, 10; V.I, 5; P.16; C.14.

Scalation.—Ll. 35-38 tr: 13-15, predorsal 25; cheek scales 5 rows; scales feebly ctenoid; markedly so on the head; with numerous (up to 12) radii and a long oblique mucous groove.

Body slender. Upper profile almost straight; lower curved; head length subequal to body depth in larger specimens; greater than the depth in specimens less than 7 cm long. Snout length equal to eye length, upper lip narrow; mouth terminal, cleft oblique, lower lip thin with a distinctly double symphysial knob; a close-set row of ciliate teeth on both jaws. Teeth on vomers, palatines, pterygoids, and tongue. Tongue with a high ridge. Posterior end of maxillae turned downwards and visible when the mouth is closed; outline of the jaw rounded, mandibulary angle almost a rectangle to obtuse. Nostrils nearer to each other than to eye and upper lip. Adipose eyelid a rudimentary rim, scarcely apparent. Interorbital distance narrow compared with most mullets. Margin of the operculum oblique. Preorbital broad, distinctly notched with 14 anterior denticulations and 8 posterior denticulations; extending under eye to mid-eye level.

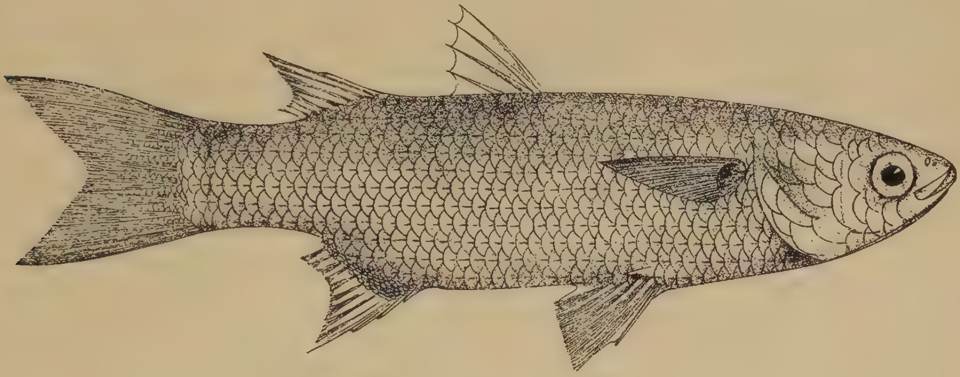

Fig. 7.—*Liza argentea* (after Tosh 1903).

The pectoral fin reaches to 12th scale and turned forward reaches more than ½ way across the eye. No axillary scale. The ventral fin relatively short, originating a little before the mid point of the pectoral and reaching the level of the base of the 2nd spine of the dorsal fin. The obbasal scale is relatively small, the interventral flange much longer. The 1st dorsal fin originates at the 13th scale; nearer snout than to the caudal base. The 2nd dorsal originates at the 23rd scale, about ½ way along the anal fins; it has a rather short base and is lower than the 1st dorsal or the anal, which are of equal height. The anal is markedly notched and the anterior rays extend back beyond the level of posterior end of the posterior rays.

Gill-rakers: 42/100; pyloric caecae 2.

Size.—Reaches to 29 cm L.C.F.

Coloration.—Predominantly silvery on sides and below; back a light brown; caudal and dorsal fins dusky, anal and pectoral less so; a patch of bright gold at the upper posterior corner of the operculum. Iris of eye purple with golden flecks.

Discussion.—As McCulloch (1921) pointed out, authors who followed the description of Gunther (1861) erred. Gunther described a fish with 9 anal rays and an adipose eyelid; whereas *argentea* has 10 anal rays and no adipose eyelid. Fowler's (1928) description differs from *argentea* in several particulars. He described the maxillae as hidden, the eye with broad adipose lids, the snout shorter than the eye, 1st dorsal commencing at 10th scale, and 2nd at 20th; only 28 lateral scales, 10 transverse and 18 predorsal, and 9 anal rays, in all of which the Samoan fish differs from the Australian. McCulloch (1921) has united *argentea* with *peronii,* the former being only the young of the latter.

The description of *Mugil convexus* De Vis (1885) agrees in all points with this species.

Material.—Australian Museum: I 15182 (Nepean R.); I 15174 (Wonboyn R.) I 7649-50, I 4452, I A 3111 (Port Jackson); I 12606 (Brisbane R.); I A 3547 (6 specimens Maroubra); I 330 (Melbourne); I 12753 (Port Stephens). Queensland Museum: I 611 (Tabbi-Tabbi, C. York, and Myora, Moreton Bay); I 1000 (Port Jackson); I 1006 (coast of Queensland). C.S.I.R.O. Marine Laboratory, Cronulla: 16 specimens from Port Adelaide; 6 specimens from Tea Gardens, Port Stephens; 4 specimens Ballina; 2 specimens Hawkesbury R. Other material: Numerous specimens from Clyde R., Hastings R., Narooma, Port Hacking, Port Macquarie, Wallis Lake, Nambucca, Richmond R., Clarence R., Tweed R., Lake Macquarie (N.S.W.); Noosa R., Moreton Bay, Mary R., Burnett R., Maroochy R. (Queensland); Mandurah; City Beach (W.A.).

6. LIZA VAIGIENSIS (Quoy & Gaimard)

Fig. 8

Mugil vaigiensis Quoy and Gaimard, 1824, p. 337, pl. 49, fig. 2 (Waigiou); Bleeker, 1859, p. 276 (East Indies); 1860*a*, p. 43 (Borneo); 1868, p. 300 (Waigiou); de Beaufort, 1913, p. 107 (New Guinea); Weber and de Beaufort, 1922, p. 244; Fowler, 1927, p. 8 (central Pacific); 1928, p. 124, fig. 27; 1931, p. 324; 1934, p. 308 (Oceania); 1935, p. 145 (Hong Kong); Schultz, 1943, p. 81 (Samoa).

Mugil macrolepidotus Rüppel, 1828, p. 140; Cuvier and Valenciennes, 1836, p. 134; Bleeker, 1854, p. 514 (East Indies); Cantor, 1850, p. 1077 (Malaya); Jouan, 1861, p. 316 (Torres Strait).

Mugil melanochir Cuvier and Valenciennes, 1836, p. 143; Bleeker, 1848, p. 5 (Madura); 1852, p. 423 (East Indies).

Mugil rossii Bleeker, 1854, p. 45; 1858, p. 276; Weber, 1913, p. 138 (East Indies); de Beaufort, 1913, p. 107 (New Guinea).

Mugil waigiensis Gunther, 1861, p. 435, fig. 9 (Red Sea; Indian Ocean; Australia; and Polynesia); 1877, p. 216, pl. 121, fig. *b* (South Pacific); 1880, p. 62 (Cape York); Day, 1865, p. 144 (Malabar); 1878, p. 359 (India); Kner, 1865, p. 226 (Pacific); Klunzinger, 1870, p. 828 (Red Sea); 1879, p. 395 (Port Dennison); 1884, p. 133 (Red Sea); Castelnau, 1875, p. 140 (Queensland); Peters, 1877, p. 842 (Indo-Pacific); Macleay, 1878, p. 359 (Darwin); 1880, p. 420 (N.S.W.; Queensland; W.A.); 1881, p. 47 (Port Jackson; Western Port); 1882, p. 362 (New Guinea); 1884*b*, p. 207 (Burdekin R.); Sauvage, 1891, p. 401 (Madagascar); Gilbert, 1891, p. 549 (California); Seale, 1903, p. 65 (Guam); 1906, p. 15 (South Pacific); Steindachner, 1906, p. 1416 (Samoa); Stead, 1907, p. 7 (Ballina; Rockhampton; Cleveland Bay); McCulloch, 1921*b*, p. 48; 1922, p. 38; 1934, p. 38, pl. 14, fig. 134*d* (N.S.W.); McCulloch and Whitley, 1925, p. 141 (Queensland); Duncker and Mohr, 1926, p. 135, figs. 4, 5 (South Pacific); Paradice and Whitley, 1927, p. 81 (Pellew Is.); Smith, 1935, p. 633, fig. 16; Marshall, 1950, p. 200 (Cocos Is.).

Mugil ventricosus Castelnau, 1875, p. 32; Macleay, 1881, p. 48; McCulloch, 1929, p. 114 (Nichol Bay); Whitley 1948*a*, p. 17 (north-west Australia).

Mugil delicatus Jouan (1878) p. 333 (Torres Strait).

Liza vaigiensis Jordan and Seale, 1906, p. 218 (Samoa); Kendall and Goldsborough, 1911, p. 257 (central Pacific); Cockerell, 1913, p. 53 (Queensland); Whitley, 1928, p. 12 (Melanesia); McCulloch, 1929, p. 116 (Queensland; NW. Australia; Northern Territory).

Liza waigiensis Seale, 1906, p. 15 (South Pacific); Reeves, 1927, p. 8 (Shanghai); Chu, 1931, p. 105 (Shanghai).

Ellochelon vaigiensis Whitley 1930, p. 250 (Waigiou); 1932, p. 338 (NW. Australia); 1948*a*, p. 17 (W.A.); Smith, 1948, p. 840; 1949, p. 320, fig. 883 (Indo-Pacific).

Type locality: Waigiou.

Vernacular name: diamond-scale mullet.

D.IV, I, 8; AIII, 8; V.I, 3; P.16; C.14.

Scalation.—L1, 25-29, tr. 10-12; predorsal 15-16; cheek scales 3. Scales large, ctenoid with 5 or 6 radii, with short oblique mucous canals.

Body robust, dorsal profile almost straight, lower curved; head length subequal to depth in specimens under 20 cm, but the relative depth of the body increases with age, relatively deep at caudal peduncle. Snout length shorter than diameter of eye in small specimens, becoming subequal in specimens 20-28 cm long and longer in older specimens. Upper lip narrow, mouth terminal, cleft oblique, lower lip thin, symphysial knob high, single; scattered fine ciliate teeth on lips, very few on lower; teeth on tongue, none on palate. Tongue slightly ridged. Posterior end of maxilla turned down and visible when mouth is closed. Mouth broadly obtuse. Nostrils with large openings closer together than to edge of lip or eye, adipose eyelid rudimentary, not obtruding onto eye. Margin of operculum oblique. Preorbital notched, denticulate, posterior margin broadly rounded. The pectoral fin reaches the 7th scale, not to origin of the 1st dorsal, and turned forward does not reach eye. No axillary scale. The ventral fin moderately long, originating about mid point of pectoral and reaching level of the base of the 2nd dorsal spine, the ventral obbasal scale is relatively large, but not as long as the interventral flange. The 1st dorsal fin originates at the 8th scale, nearer to the caudal base than to the snout. The 2nd dorsal originates at the 17th scale, ½ way along the anal scale. The anal height is greater than the height of the 2nd dorsal, higher than the 1st dorsal. The 2nd dorsal, anal, and caudal are only slightly emarginate. Second dorsal and anal scaly.

Gill-rakers 32/58; pyloric caecae 10.

Size.—Reaches to 55 cm L.C.F.

Coloration.—Light olive above, silvery on the sides, with a yellowish wash below. Margin of fins dusky; otherwise yellowish white; pectoral wholly black in young specimens; lower margin yellow in adults. Iris with yellow patches. Upper lateral rows of scales with brown spots, giving the effect of longitudinal bands.

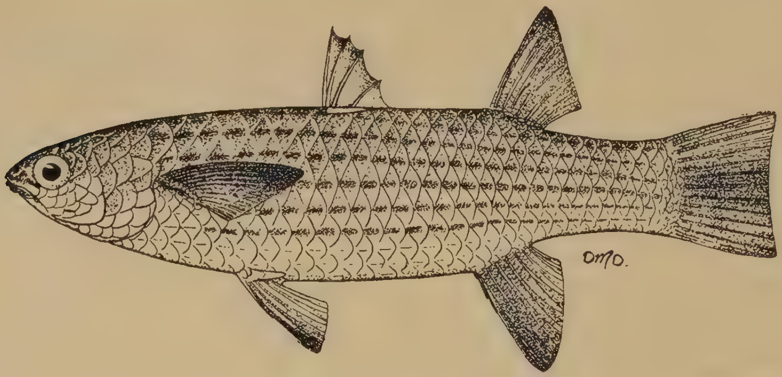

Fig. 8.—*Liza vaigiensis* (after Smith 1949).

Discussion.—Several authorities, including Whitley (1930), Smith (1948, 1949), Gunther (1861), and Weber and de Beaufort (1922), stated that there is no adipose eyelid. Nevertheless distinct patches of gelatinous adipose tissue are present both in front of and behind the eye; however, they do not intrude upon the eye.

As Whitley (1932) noted, there does not seem to be any real difference between *Mugil ventricosus* Castelnau and *Liza vaigiensis* which could not be accounted for as a result of distortion, preservation, and storage. In description the species does not seem to differ much from *Mugil oligolepis* Bleeker except that the latter species is recorded as having 9 anal rays instead of 8.

Material.—Australian Museum: 383 (Burdekin R., Queensland); I 9708, I 11154 (Cape York); I 14493 (Cooktown) (2 spec.); I 15171-2 (Wide Bay, Queensland); IA 2368-70 (Cumberland I., Great Barrier Reef); IA 3046 (Brampton I., Mackay); IA 4465 (Low I., Great Barrier Reef—2 spec.); IA 4609 (North-west Islet, Queensland); IA 6140

(Lindeman I., Queensland—10 spec.); IA 6644 (Cape Gloucester, Queensland—2 spec.); IB 796 (Richmond R., N.S.W.); IA 1448-9, IA 1470 (Pellew Group, Gulf of Carpentaria); IA 4677, IB 616 (Darwin); IA 7613-5 (Melville I.—6 spec.); IA 7674-6 ("Northern Territory"); I 9186 (Port Moresby) IB 1514 (Bat I., Purdy Archipelago, N.G.); B 8002 (Madras); (I 6575) I 13754-7 (New Hebrides); I 15188 (Guadalcanal); I 10579-80 (Sitanki I., Jolo Archipelago); IA 2862 (Peu, Vanikoro); IA 4702 (Ellice Is.); IA 7145 (Nauru). Other material: Specimens from Prince of Wales I., Thursday I., Yeppoon, Queensland, Exmouth Gulf, Broome, W.A.

7. LIZA RAMSAYI (Macleay)

Fig. 9

Mugil ramsayi Macleay, 1883, p. 208; 1885, p. 42 (Burdekin R.); McCulloch, 1929, p. 116; McCulloch and Whitley, 1925, p. 141 (Burdekin R.).

Gracilimugil ramsayi Whitley, 1941, p. 19, fig. 14.

Trachystoma ramsayi Schultz, 1946, p. 392.

Type locality: Burdekin R., Queensland. Lectotype Australian Museum.

D.IV, I, 8-9; A.III, 10-11; V.I, 5; P.I, 15; C.16.

Scalation.—L1, 36-37, tr. 13-15, predorsal 24, cheek scales in 5 rows. Scales cycloid dorsally, feebly ctenoid laterally and more definitely ctenoid ventrally, 4-5 radii and a short straight mucous groove.

Body moderately robust, compressed as preserved; head rather shallow, upper profile gently convex, the ventral more markedly so. Head length greater than the depth. Diameter of the eye greater than length of the snout. Upper lip moderately thick; mouth terminal; cleft slightly oblique, lower lip thin with a feebly double symphysial knob. A close-set row of ciliate teeth on both lips. Teeth on vomers, palatine, pterygoids, and tongue; the tongue has a moderately high ridge. The posterior end of the maxilla turned downwards and visible when the mouth is closed. Outline of jaw rounded; mandibulary angle slightly less to slightly more than rectangular. Nostrils nearer each other than to eye or upper lip, adipose tissue in front of and behind eye, but not extending on to eye itself. Interorbital distance only moderate; margin of operculum at pectoral base, vertical, steeply sloping below. Preorbital emarginate but scarcely notched—moderately broad, up to 20 anterior denticulations—becoming smaller anteriorly, 5 posterior denticulations, and dorsally above the last of the posterior denticulations are 2 more.

The pectoral fin reaches the 10th scale, some distance in front of the 1st dorsal fin and turned forwards reaches ½ way across the eye. A small axillary scale. The ventral fins short, the obbasal relatively short, the interventral flange much longer. The 1st dorsal originates at the 13th scale, and has a long obbasal scale. The 2nd dorsal originates at the 23rd scale, about ½ way along the anal fin, which is higher than the dorsal fins, which are subequal in height.

Size.—The largest specimen seen measured 26.1 cm L.C.F.

Coloration.—(In formalin) silvery with a bluish brown back.

Discussion.—This species is very similar to *Liza argentea* and may be a tropical variant. The chief differences are the presence of an axillary scale (though a small one) in *ramsayi*, a greater variability in anal and 2nd dorsal ray number, the rather thicker upper lip, the more robust body, and the fewer denticulations on the preorbital.

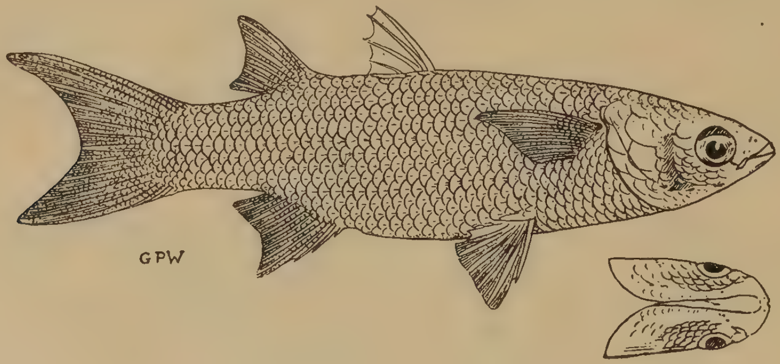

Fig. 9.—*Liza ramsayi* (after Whitley 1941).

Whitley (1941) said *ramsayi* has no axillary scale; but Macleay (1883) recorded its presence, and it is present in the type specimens. Although Whitley described the upper lip as thick, Macleay called it thin and in fact it is only moderately thick, no thicker than in *Mugil cephalus*. Macleay recorded 8 dorsal rays; Whitley 9; Whitley also recorded 11 anal rays. There are 7 specimens in the type collection labelled IA 5944-6 (Australian Museum). The lectotype (IA 5944), measuring 26.1 cm L.C.F., has 9 dorsal rays and 11 anal; 5 of the others measuring 22.2, 19.0, 11.9, 11.6 cm have 9 dorsal rays and 10 anal; and 1 specimen 10.6 cm L.C.F. has 8 dorsal rays and 10 anal.

Material.—Australian Museum: IA 5944-6. 7 specimens Burdekin R., Queensland.

8. LIZA DIADEMA (Gilchrist & Thompson)

Fig. 10

Mugil diadema Gilchrist and Thompson, 1911, p. 42; 1917, p. 273 (Natal); Barnard, 1925, p. 309 (Natal).

Mugil macrolepis Boulenger, 1916, p. 94 (partim) (Natal).

Mugil compressa Smith, 1935, p. 626, fig. 13 (Port Elizabeth, Durban) (non Gunther 1861).

Moolgarda (*Planiliza*). *ordensis* Whitley, 1945, p. 17, fig. 9 (Ord R., north-west Australia); 1948*a*, p. 17.

Pteromugil diadema Smith, 1948, p. 827, fig. 6; 1949, p. 319, fig. 881.

D.IV, I, 8; A.III, 9; P.16; C.12.

Scalation.—L1, 30-31, tr. 11-21; 7 rows down caudal peduncle; predorsal 18—cheek scales 4-5 rows; scales feebly ctenoid to cycloid, except the predorsal and ventral scales, which are markedly ctenoid, each with 4 or 5 radii and an elongate oblique mucous canal.

Body moderately deep, compressed towards the tail; head profile acutely angled, convex dorsally and ventrally. Head length subequal to body depth; eye diameter less than snout length. Upper lip thin, mouth terminal, cleft oblique, lower lip thin with a rounded symphysial knob. Thin ciliate recurved teeth in 2 rows on upper lip, lower lip edentate, pterygoids and tongue with villiform teeth; vomers and palatines edentate. Posterior end of maxilla bent down and exposed. Outline of lower jaw rounded, mandibulary angle obtuse. Nostrils closer together than to the eye or upper edge of lip. Adipose tissue slight, forming an insignificant rim around eye and extending to the posterior nostril on the face and an equal distance in a triangular patch behind the eye. Head and interorbital width rather great. Margin of operculum at pectoral level, oblique with a marked backward projection over the base of the pectoral. Preorbital slightly emarginate, but scarcely notched; well denticulated, rather truncate posteriorly.

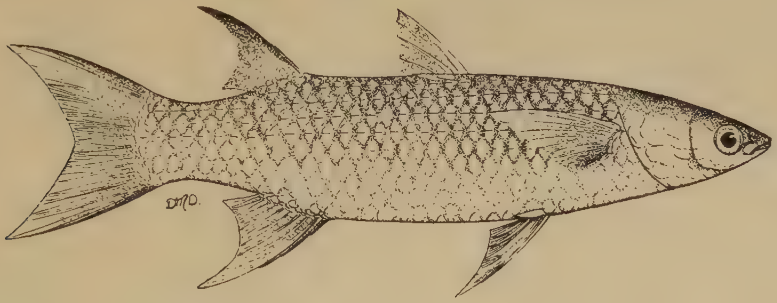

Fig. 10.—*Liza diadema* (after Smith 1949).

The pectoral fin, which has no axillary scale, reaches the 8th body scale; turned forwards reaches ½ way across the eye; does not reach the 1st dorsal fin, which originates at the 10th scale; nearer the snout than the caudal base. The 2nd dorsal origin is at the 20th scale, about ½ way along the anal fin, which is short-based and higher than the dorsal fins, which are subequal in height. The ventrals rather long, the interventral flange larger than the obbasal. The caudal is deeply forked, the upper lobe being longer than the lower.

Gill-rakers: 22/64; pyloric caecae 5.

Coloration.—Light brown dorsally, silvery laterally: dark streaks on upper rows of scales, fins greyish.

Discussion.—Comparison of South African specimens of *diadema* with specimens of *ordensis* shows no apparent differences, except that the fins are more falcate in the South African fish.

Material.—Australian Museum: IA 7913 (Melville I.); IA 7633-37 ("Northern Territory"); 2 specimens of *Pteromugil diadema* from South Africa. Perth Museum: P. 2758 (Ord R.); P. 2487-8 (Exmouth Gulf); P. 175 (Broome).

9. VALAMUGIL SEHELI (Forskal)

Plate 2, Fig. 1

Mugil crenilabis seheli Forskal, 1775, p. 73 (Lokajae, Red Sea).

Mugil seheli Klunzinger, 1870, p. 827; 1884, p. 132 (Red Sea); Day, 1878 p. 385; Weber, 1913, p. 140 (East Indies); Boulenger, 1916, p. 91, fig. 63 (South Africa); Weber and de Beaufort, 1922, p. 252 (Indian Ocean-West Pacific); Fowler, 1925*b*, p. 32; (Samoa, Hawaii); 1928, p. 125 (Oceania); 1930, p. 603 (Hong Kong); 1931, p. 324 (Oceania); 1934, p. 309 (Oceania); 1935, p. 143 (Hong Kong); Norman, 1930, p. 616 (Suez Canal); Smith, 1935, p. 621, fig. 11 (Durban); Schultz, 1943, p. 81; Marshall, 1950, p. 170 (Cocos Is.).

Mugil caeruleomaculatus Lacepede, 1803, p. 285 (Mauritius); Cuvier and Valenciennes, 1836, p. 178 (East Indies); Bleeker, 1851, p. 484 (Borneo); 1858, p. 279 (East Indies); 1860*b*, p. 5 (Sumatra); 1868, p. 300 (Waigiou); 1878, p. 38 (New Guinea); Gunther, 1861, p. 445; Sauvage, 1891, p. 398 (Madagascar); Weber and de Beaufort, 1922, p. 250 (East Indies, Malaya, Madagascar); Duncker and Mohr, 1926, p. 131 (Hunsa Bay, New Guinea); Marshall, 1950, p. 170 (Cocos Is.); 1951, p. 6, pl. 3, fig. 2 (Cape York).

Mugil axillaris Cuvier and Valenciennes, 1836, p. 139; Bleeker, 1858, p. 280 (East Indies); 1860*b*, p. 3 (Sumatra); 1873, p. 143 (Amoy); Gunther, 1861, p. 444 (East Indies); 1880, p. 216 (South Pacific); Kner, 1865, p. 227, pl. 9, figs. 3-9 (Shanghai); Alleyne and Macleay, 1877, p. 341 (New Guinea); Macleay, 1882, p. 362 (New Guinea); Sauvage, 1891, p. 397 (Madagascar); Seale, 1901, p. 66 (Marianas, Samoa); Chu, 1931, p. 105 (China).

Mugil melanicranus Richardson, 1846*b*, p. 248 (Canton); Gunther, 1861, p. 410 (China); Bleeker, 1873, p. 143 (China); Chu, 1931, p. 105 (China).

Mugil parsia Bleeker, 1852 (East Indies) (non Hamilton 1822).

Mugil cylindricus Bleeker, 1853, p. 266 (Java).

Mugil borbonicus Bleeker, 1858, p. 279; 1859, p. 375 (East Indies).

Mugil bleekeri Gunther, 1861, p. 445 (East Indies); Weber 1895, p. 416 (East Indies); de Beaufort, 1913, p. 107 (East Indies).

Mugil decem-radiatus Gunther, 1861, p. 452 (East Indies).

Mugil delicatus Alleyne and Macleay, 1877, p. 341 (Cape York). Macleay, 1880, p. 422 (Cape York); 1881, p. 48 (Cape Grenville); McCulloch, 1929, p. 114 (Cape York); McCulloch and Whitley, 1925, p. 141 (Cape York, Cape Grenville); Whitley, 1932, p. 280 (Great Barrier Reef).

Liza caeruleomaculatus Jordan and Seale, 1906, p. 217 (Samoa); Jordan and Dickerson, 1908, p. 607 (Fiji); Kendall and Goldsborough, 1911, p. 256 (tropical Pacific).

Liza seheli Herre, 1932, p. 3 (Tahiti).
Valamugil seheli Smith, 1948, p. 840 (South Africa); 1949, p. 323, fig. 889 (South Africa).

Type locality: Lokajae, Red Sea. (No type specimen.)

Vernacular names: blue-spot, or blue-tail mullet.

D.IV, I, 8; AIII, 9; V.I, 5; P.16.

Scalation.—Ll, 38-42, tr. 12-14, predorsal 22-23; cheek scales 3. Scales feebly ctenoid, 6 radii and an elongate slightly oblique mucous groove.

Body robust. Upper profile gently convex; head length equal to or slightly greater than depth in young specimens (under 12 cm), but distinctly less than the depth in older specimens. Eye diameter greater than snout length. Upper lip moderately broad—mouth terminal, cleft oblique, lower lip thin with a double symphysial knob. No teeth on lips, but some on vomers and palatines. Posterior end of maxilla slightly turned down but not visible when the mouth is closed. Outline of jaw angular, mandibulary angle obtuse. Nostrils nearer each other than to upper lip or eye. Adipose eyelid rudimentary, not obtruding onto eye. Head width and interorbital width relatively great. Margin of operculum at pectoral level slightly oblique. Preorbital notched only in specimens less than 25 cm L.C.F., the notch and the denticulations become obscured in older specimens. The hind end of the preorbital scarcely reaches the anterior edge of the eye.

The pectoral fin reaches to the 12th to 14th scale beyond the origin of the 1st dorsal fin and beyond the spine of the ventral fin. In very large specimens, the pectoral may not reach the dorsal. Turned forward the pectoral reaches in front of the snout tip. There is a large axillary scale. The ventral fins relatively long, with long obbasal scale and interventral flange; the obbasal being longer than the interventral. The 1st dorsal fin originates at the 10th to 13th scale, about midway between tip of snout and caudal base. The dorsal obbasal scale is unusually long. The 2nd dorsal origin is at the 22nd or 23rd scale almost opposite the origin of the anal. Second dorsal and anal scaly, falcate, very high, considerably higher than the 1st dorsal. The caudal strongly forked, the upper lobe the longer.

Gill-rakers: 28/56; pyloric caecae 2.

Coloration.—Greenish-brown dorsally; silvery below, upper rows of scales with dusky spots forming indistinct bands. Soft dorsal and caudal a pale blue, ventral, anal, and 1st dorsal white, pectoral dull yellow. Upper lobe of caudal with a dark blue tip and the pectoral with a marked blue axillary spot. Iris silvery brown.

Discussion.—Despite the merging of *Mugil caeruleomaculatus* Lacepede with *Mugil seheli* Forskal, by certain authorities, including Fowler (1928), others, notably Weber and de Beaufort (1922) and Smith

(1935), have maintained their separate identities. The descriptions of the 2 species by Weber and de Beaufort show no differences of any significance—in fact most of the descriptions are identical. Smith stated that South African specimens of *seheli* differed from an Indian specimen of *caeruleomaculatus* but did not state in what particulars. As stated above there is considerable change in proportions as size increases, so that small specimens such as Smith recorded might vary considerably from older fish. On the other hand Smith described the tongue as having patches of teeth; this is not so in the Indo-Pacific forms described here. Unfortunately few authorities prior to Smith examined the dentition of the palate and the tongue. There may remain a doubt whether *seheli* and *caeruleomaculatus* are identical. But there can be no doubt that Marshall (1951) was correct in assigning *Mugil delicatus* Alleyne and Macleay to *caeruleomaculatus*. Indian and Oceanic specimens of the latter species show no differences from *delicatus* of the same size. Jordan and Seale (1906) listed *Agonostomus dorsalis* Streets (1877) as a synonym of *caeruleomaculatus*. Schultz (1946) examined the type of *A. dorsalis* and referred it to his genus *Chelon*, which has an exposed maxillary. Also according to Schultz (1943) this species has only 33 lateral scales and therefore cannot be *seheli* (38-42 scales); but may be *Liza troscheli*.

Material.—Macleay Museum Sydney: type (F 374—No. 306) and cotypes of *Mugil delicatus* (Cape York). Australian Museum: I 11890-8 (Cape York); IA 2076 (Great Barrier Reef); I 10507, I 10529 (Mindanao); I 7775-9 (Samoa); B 8036 (Bombay). Queensland Museum: I 3966, I 996 (Cape York); 113/967 (type of *Mugil splendens*). Other material: Several specimens from Princess Charlotte Bay; 3 specimens from Darwin.

10. VALAMUGIL BUCHANANI (Bleeker)

Plate 2, Fig. 2

Mugil buchanani Bleeker, 1853, p. 99 (Hooghly R.); Day, 1878, p. 358 (India); Pellegrin, 1898, p. 229 (Marianas); Fowler, 1928, p. 123 (Marianas); Smith, 1935, p. 623, fig. 12 (Knysna, Durban, Chinde, Celebes).

Mugil ceylonensis Gunther, 1861, p. 446 (Ceylon); Boulenger, 1916, p. 93, fig. 55 (East Africa); Barnard, 1925, p. 305 (East Africa).

Valamugil buchanani Smith, 1948, p. 841, fig. 13; 1949, p. 323, fig. 888 (South-east Africa).

Type locality: Hooghly River.

D.IV, I, 8; A.III, 9.

Scalation.—L1, 34-36, tr. 11-13, predorsal 18, cheek scales 3-4 rows. Scales ctenoid, with scalloped edge, 5-6 radii, and a very thin, long, slightly oblique mucous groove.

Body robust, head length equals the depth; the snout is wide, broadly rounded dorso-ventrally, and shorter than the eye diameter. Upper lip thin, mouth terminal, cleft almost horizontal; lower lip thin with a double symphysial knob. A row of small ciliate teeth in both lips—tending to disappear in adults. Teeth on pterygoids and on tongue but none on palatine or vomer. Maxilla curves downwards slightly but is hidden when the mouth is closed. The mouth has an angular outline and the mandibulary angle is obtuse. The adipose eyelid is an obsolescent rim extending slightly on the face. Head of moderate width. Margin of the operculum very slightly oblique at the pectoral level—no backward projection. The preorbital is slightly notched, with a narrow posterior edge, denticulated.

The pectoral fin reaches the 10th or 11th scale—behind the origin of the 1st dorsal fin, turned forward the fin reaches in front of the eye; axillary scale moderate. The ventrals are much shorter than the pectorals, and originate nearer to the level of the origin of the 1st dorsal than to the head. The moderate obbasal and interventral flange are equal in length. The 1st dorsal originates at the 9th or 10th scale, nearer the snout than the caudal base. The obbasal is moderately long—reaching behind the base of the 4th spine. The 2nd dorsal originates at the 19th to 22nd scale, opposite the origin of the anal. Fins high, 2nd dorsal, anal, and caudal markedly emarginate in adults, feebly emarginate in smaller specimens. Second dorsal and anal fins scaly.

Length.—Up to 40 cm.

Coloration.—Greenish above, silvery on sides and beneath. Dark axillary spot on pectoral; yellowish on operculum and on iris.

Discussion.—Only 1 Australian specimen is identified as this species; it has been compared with a specimen from South Africa supplied by Dr. J. L. B. Smith and with a specimen from Amboina in the Australian Museum.

Material.—W.A. Museum: P 3474 ("north-west"). Australian Museum: I 94 (Amboina). Other material: Durban, South Africa.

11. TRACHYSTOMA PETARDI (Castelnau)

Fig. 11

Mugil breviceps Steindachner, 1866, p. 459, pl. 1, fig. 1 (non Cuvier and Valenciennes 1836).

Mugil petardi Castelnau, 1875, p. 32 (Roebuck Bay); Waite, 1904, p. 22 (Richmond R.).

Mugil pettardi Macleav, 1880, p. 422 (N.S.W.); 1881, p. 48 (Richmond R.), Ogilby, 1887, p. 27 (Richmond R.).

Trachystoma multidens Ogilby, 1887, p. 614 (Karuah R., Port Stephens); Waite, 1904, p. 22.

Liza breviceps Tosh, 1903, p. 3, pl. 2, fig. 4 (Nerang R., Queensland).

Mugil parviceps Waite, 1904, p. 22.

Trachystoma petardi Ogilby, 1908, p. 28; 1915, p. 7 (Queensland); McCulloch, 1921*b*, p. 49; 1922, p. 39; 1929, p. 118; 1934, p. 39, pl. 14, fig. 142*a*. (N.S.W. rivers north of Sydney); McCulloch and Whitley, 1925, p. 141 (Nerang R.); Schultz, 1946, p. 392 (Clarence R.).

Type locality: Roebuck Bay.

D.IV, I, 8; A.III, 9; V.I, 5; P.15; C.14.

Scalation.—L1, 47-50 tr. 15-16. Predorsal 29-30; cheek scales 5. Scales ctenoid; 3-4 radii, a small mucous groove.

Body robust; deep-bellied, head length less than depth; the head strongly pointed; snout length slightly greater than the eye diameter. Upper lip thin, mouth terminal, cleft oblique, lower lip thin with a double symphysial knob. A row or rows of fine ciliate teeth embedded in both lips and projecting only slightly, teeth on vomer, palatines, pterygoids, and tongue. End of maxilla usually hidden when mouth is closed, visible in some specimens, but the maxilla is not bent downwards, mouth rather angular, the mandibulary angle slightly obtuse. Nostrils closer together than to the edge of the lip or to the eye. Adipose eyelid absent. Head wide at the posterior end but the interorbital narrower in proportion to the width than in other Australian mullets. Margin of the operculum at the level of the pectoral base oblique. The preorbital is not notched and is almost straight-edged, with a broad posterior edge bearing more denticulations than the ventral edge.

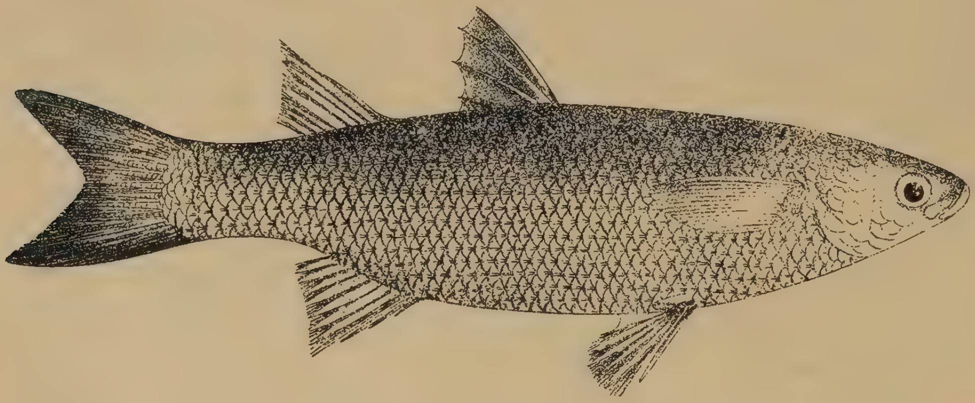

Fig. 11.—*Trachystoma petardi* (after Tosh 1902).

The pectoral fin reaches the 13th or 14th scale, not nearly to the 1st dorsal origin, turned forward just reaches to the hind edge of the eye. No axillary scale. Ventrals almost as long as the pectoral, the ventral obbasals are rather short, but the interventral flange is longer. The 1st dorsal fin originates at the 19th or 20th scale and the 2nd at the 32nd to 34th scale, ½ way along the anal fin. The unpaired fins are relatively high, the anal and 1st dorsal about equal, the 2nd dorsal somewhat lower. The fins other than the 1st dorsal are extensively scaled. Caudal fork slight.

Length to 40 cm.

Coloration.—Dark olive-green above, silvery below, fins pale yellow, upper edge of operculum golden; iris golden. No pectoral axillary spot.

Discussion.—As indicated by Ogilby (1908) and McCulloch (1921*b*) *breviceps* Steindachner and *multidens* Ogilby are synonyms of *petardi*. *Mugil parviceps* Waite was a nomen novum for *breviceps* Steindachner, which Waite showed to be preoccupied by *breviceps* Cuvier and Valenciennes (1836).

This species is an inhabitant of fresh to brackish waters of the east coast rivers of northern New South Wales and southern Queensland.

Material.—Australian Museum: I 13007 (Sackwell, Hawkesbury R.); I 13020-22 (Penrith, Nepean R.); I 15175-81 (Nepean R.); I 1333 (Georges R.); I 13590 (Port Macquarie); I 7648 (Clarence R.). Queensland Museum: I 4776 (Moreton Bay ?); I 4958-67 (Nerang R.). Other material: About 200 specimens from Upper Albert R., and others from the upper Logan R., the Pine R., Upper Noosa R., all in southern Queensland, and the Richmond R., N.S.W.

12. MYXUS ELONGATUS Gunther

Fig. 12

Myxus elongatus Gunther, 1861, p. 466 (Hobson's Bay and Port Jackson); 1880, p. 33 (Mary R., Queensland); Castelnau, 1879*a*, p. 386 (Port Jackson); Macleay, 1880, p. 426; 1881, p. 48; Ogilby, 1887, p. 27 (Hobson's Bay and Port Jackson); 1893, p. 128, pl. 33 (N.S.W.); 1897*a*, p. 79 (Derwent R.); Tosh, 1903, p. 3, pl. I, fig. 4. (Wide Bay; Moreton Bay); Waite, 1904, p. 23 (N.S.W.); 1916, p. 454, pl. 44 (S.A., N.S.W.); 1921, p. 84, fig. 27 (S.A.); 1923, p. 108 (S.A.); 1928, p. 6 (S.A.); Stead, 1908, p. 15 (N.S.W.); Roughley, 1916, p. 43, pl. 9 (N.S.W.); McCulloch, 1921*a*, p. 49 (N.S.W.); 1921*b*, p. 132 (N.S.W.; Vic.; S.A.); 1922, p. 39; 1929, p. 118; 1934, p. 39, pl. 14, fig. 140*a* (N.S.W.); Weber and de Beaufort, 1922, p. 266 (East Indies); McCulloch and Whitley, 1925, p. 141 (Mary R., Moreton Bay); Fowler, 1934, p. 309 (Oceania); Schultz, 1946, p. 389.

Mugil crenidens Kner, 1865, p. 229, pl. 9, fig. 4 (Oceania).

Myxus crenidens Steindachner, 1866, p. 461.

Cestraeus norfolcensis Ogilby, 1897*b*, p. 80.

Type localities: Hobson's Bay and Port Jackson. Type specimen British Museum.

Vernacular names: sand mullet, tellegalene, tallegalane.

D.IV, I, 8-9; A.III, 9; V.I, 5; P.16; C.15.

Scalation.—L1, 43-46, tr. 15-16; cheek scales 5; predorsal 28. Scales cycloid, with up to 12 radii and an oblique mucous groove.

Body slender, lower profile gently convex, upper profile almost straight. Head length rather longer than the depth of the body. Eye diameter considerably less than the snout length. Upper lip thin subterminal; lower lip horizontal subventral fitting below the upper lip; symphysial knob feebly double; each lip with a single row of small incisor-like teeth, which are close together. Teeth on vomers and palatines, but not on pterygoids and tongue. The maxillary is not bent down and the posterior end is usually hidden when the mouth is closed, in some specimens a small part of the end is visible and a narrow strip of the maxilla may be visible dorsally above the premaxilla. The outline of the jaw angular, the mandibulary angle acute in small specimens, but obtuse in examples over 20 cm L.C.F. Nostrils nearer each other than to eyes or upper lips. Adipose eyelid absent. Head of only moderate width. Operculum at pectoral base level is almost vertical. Preorbital almost straight or with a very slight emargination, but not notched, more denticulations on the ventral edge than on the posterior.

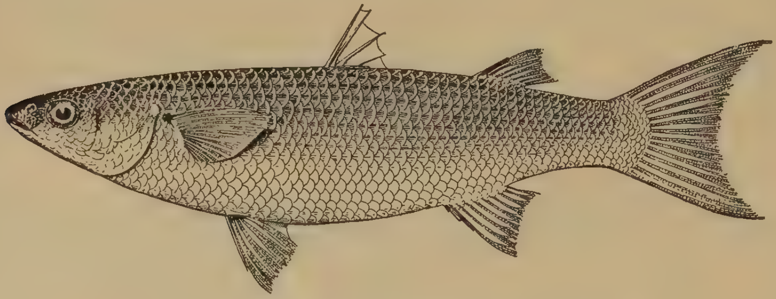

Fig. 12.—*Myxus elongatus* (after Waite 1916).

The pectoral fin reaches to 12th or 13th scale, not to 1st dorsal origin, and turned forwards reaches about $\frac{1}{4}$ of the way across the eye. There is no axillary scale. The 1st dorsal origin is at the 16th scale, the 2nd dorsal at the 29th or 30th scale, behind the origin of the anal fin, which is higher than the 2nd dorsal, which is slightly higher than the 1st dorsal. Ventrals rather small. Dorsal and ventral obbasals of only moderate length; and the interventral flange longer than the ventral obbasal.

The fins are not scaly. The anal is well notched, the anterior rays extending back almost as far as the posterior rays; the caudal is deeply forked.

Coloration.—Dark olive-green dorsally, silvery laterally, white ventrally. Pectoral, dorsal, and caudal fins dusky, anal white-edged. Iris yellow with iridescent hues. A dark pectoral axillary spot.

Size.—Attains a size of at least 25 cm.

Discussion.—The synonymy of this species has been dealt with by Waite (1904) and McCulloch (1921*b*). However, examination of the type of Ogilby's *Cestraeus norfolcennis* (I 4937 Australian Museum) reveals reason to doubt the correctness of putting this species in the synonymy of *Myxus elongatus*. The specimen has only 38 lateral row scales and only 13 transverse rows; the tongue has teeth upon it, the eye length equals snout length, which is relatively long; the depth relative to length is less; the peduncle depth is considerably greater; D/P.D. = 1.95 compared with 2.65-4.43 in specimens of *Myxus elongatus*; the pectoral and ventral fins are shorter than in *Myxus elongatus* of a similar size.

Material.—Australian Museum: I 3290 (New Hebrides); I 3580 (Funafuti); I 4619 I 5586-9 (Lord Howe I.); I 6994 (Mandurah, W.A.); I 9511 (Sydney); A 5940-1 (Tas.); IA 1854-5 (Shell Harbour, N.S.W.); IA 3248 (Watson's Bay); IA 3935, IA 6606 (Maroubra); IA 4866 (Manly); IA 7044 (Brunswick Heads); IA 7070 (Port Jackson); IA 7981 (Noosa R., Queensland); IB 2564 (Mona Vale, N.S.W.); IB 997 (Coolangatta, Queensland); IB 998 (Tweed Heads). Queensland Museum: I 1487 (Noosa R.); I 2634, I 3840 (Cowan Cowan). W.A. Museum: 107 (Mandurah). Other material: Numerous specimens from Lake Merimbula, Yamba, Nambucca, Port Jackson, Tuggerah Lakes, Richmond R., Pittwater, Bellingen R. (all N.S.W.); Southport, Myora, Stradbroke I., Caloundra (Queensland), Whitford's Beach, Scarborough (W.A.).

13. ALDRICHETTA FORSTERI (Cuvier & Valenciennes)

Plate 2, Fig. 3

Mugil forsteri Cuvier and Valenciennes, 1836, p. 141 (N.Z.).

Mugil albula Forster, 1844, p. 145 (N.Z.) (non Linnaeus 1758).

Dajaus diemensis Jenyns, 1842, p. 82 (King George Sound); Richardson, 1839, p. 37, pl. 16, figs. 1-4; 1846*b*, p. 25 (Port Arthur, Tas.).

Agonostomus forsteri Gunther, 1861, p. 465 (N.S.W.); Steindachner, 1866, p. 460 (Port Jackson, Hobson's Bay, N.Z.); 1879, p. 5 (S.A.); Castelnau, 1872, p. 141; 1873, p. 136 (Vic.); Klunzinger, 1872, p. 33 (S.A.); 1879, p. 396 (Port Phillip, Hobson's Bay, King George Sound); Thomson, 1892, p. 211 (N.Z.); Waite, 1904, p. 23 (N.S.W.); 1921, p. 83, fig. 126; 1923, p. 108; 1928, p. 6 (S.A.); Stead, 1908, p. 46 (N.S.W.); Phillipps, 1921, p. 120; 1927*a*, p. 30; Phillipps and Hodgkinson, 1922, p. 98 (N.Z.); McCulloch, 1921*b*, p. 49; 1922, p. 39 (N.S.W.); 1929, p. 118 (N.S.W., Vic., S.A., W.A., Tas.); 1934, p. 39, pl. 14, fig. 141*a* (N.S.W.).

Agonostomus lacustris Castelnau, 1872, p. 142 (Gippsland Lakes).

Agonostomus tasmaniensis Castelnau, 1872, p. 142 (nom. nov. for *Dajaus diemensis* Richardson).

Agonostoma diemensis Castelnau, 1873, p. 161; Macleay, 1880, p. 425; 1882, p. 48 (Tas.).

Aldrichetta forsteri Whitley, 1945, p. 19, fig. 10; 1948*a*, p. 17 (W.A.).

Type locality: "New Zealand".

Vernacular names: yellow-eye mullet (N.S.W., W.A.), sea mullet (Vic.; S.A., Tas., N.Z.), conmuri (S.A.), pilchard (W.A.), herring (N.Z.).

D.IV, I 9; A.III, 12.

Scalation. L1, 54-58 + 4-5, tr. 14-15, predorsal 30-31 reaching to above eye; cheek scales large, 2-3 rows. Scales cycloid except on cheek, 10-11 radii; mucous canal short, oblique.

Body slender, head length slightly greater than the body depth. Snout and eye subequal—lips thin, mouth terminal; cleft oblique, lower lip with a single low symphysial knob; fine ciliate teeth in both jaws, becoming more sparse with age—usually more evident on the lower jaw than the upper. Teeth on vomer, palatine, pterygoid, and tongue. Maxilla not bent downwards, its end hidden when mouth is closed, but a thin strip may be visible dorsal to the premaxilla. Mouth outline angular, mandibulary angle acute. Nostrils nearer each other than to upper lip or eye. Adipose eyelid present only as a slight triangular deposition in front of the eye. Head width and interorbital narrow, compared with most mullet. Margin of the operculum at the pectoral level almost vertical, without a backwardly directed projection over the pectoral base. The preorbital is not notched, is rounded anteroventrally. There are about 14 teeth on the ventral and posterior edges, and there are 3 teeth above the posteriormost tooth of the preorbital edge.

The pectoral fin reaches the 16th scale, not to the dorsal origin, turned forward it reaches ½ way across the eye. There is no axillary scale. Ventrals very short, not nearly as long as the pectorals. The ventral obbasals are unusually long, and are slightly longer than the interventral flange. The 1st dorsal fin originates at the 18th or 19th scale, and has a very short base, and a small obbasal scale. The 2nd dorsal origin is at the 34th or 35th scale, only a little behind the anal origin. The anal height is greater than that of the 2nd dorsal, which is higher than the 1st dorsal. The fins are not scaly; the caudal, 2nd dorsal, and anal are only feebly emarginate.

Gill-rakers 19/24; pyloric caecae 2.

Coloration.—Olive-brown above, silvery to yellowish white on sides and belly, fins with brownish margins. Eyes with yellow iris, no axillary spot on pectorals.

Size.—Attains at least 38 cm L.C.F.; though rarely seen above 32 cm.

Discussion.—As Whitley (1945) averred, this salt and brackish-water species cannot be included in the freshwater genus *Agonostomus*. *Aldrichetta forsteri* has thin lips compared with thick lips of *Agonostomus*; it has teeth on pterygoids and tongue, the teeth in the jaws are simple; the number of rays in the 2nd dorsal and fins exceeds that in *Agonostomus* species, and finally the stomach is gizzard-like, which it is not in *Agonostomus*.

Material.—Australian Museum: I 6281-4 (Tamar R., Tas.); I 10 (Coonong R., S.A.); I 14185 (Port Arthur, Tas.); I 13231 (Fremantle, W.A.); I 14751 (Porto Bello, N.Z.); IA 657 (King George Sound, W.A.); IA 7212 (Swan R., W.A.); IB 798 ("Tasmania"); IB 1845 (Point Cook, Vic.). W.A. Museum: P 354 (Bremer Bay); P 341 (Garden I.); P 141 (Swan R.); P 2690-2 (Leschenault Estuary, W.A.). Other material: Some thousands of specimens from all W.A. rivers south of Geraldton; from Ceduna and Port Adelaide, S.A.; Port Phillip Bay and Lakes Entrance, Vic.; Port Arthur, Pittwater, Fortescue Bay, Spring Bay, Swansea, Norfolk Bay, Tas.; Moruya, Merimbula R., N.S.W.; Waikato R., N.Z.

14. CRENIMUGIL CRENILABIS (Forskal)

Fig. 13

Mugil crenilabis crenilabis Forskal, 1775, pp. 14, 73 (Red Sea).

Mugil crenilabis Bonnaterre, 1780, p. 180; Rüppell, 1835, p. 132; Gunther, 1861, p. 458; Klunzinger, 1870, p. 827; 1884, p. 133, pl. 10, fig. 2 (Red Sea); Ogilby, 1906, p. 9 (southern Queensland); de Beaufort, 1913, p. 108 (New Guinea); Weber and de Beaufort, 1922, p. 236 (East Indies); Norman, 1922, p. 319 (Natal); Fowler, 1927, p. 10 (Pacific); 1928, p. 126; 1931, p. 324; 1934, p. 309 (Oceania); 1935, p. 146, fig. 56 (Macao); Fowler and Bean, 1927, p. 14 (Sumatra, Java); Whitley, 1927*b*, p. 11 (Michaelmas Bay); 1928, p. 12 (Santa Cruz Archipelago); Smith, 1935, p. 609 (Durban); 1937, p. 172 (Durban); Schultz, 1943, p. 81 (Samoa); Marshall, 1950, p. 169 (Cocos Is.).

Mugil cirrhostomus Bloch and Schneider, 1801, p. 121; Cuvier and Valenciennes, 1836, p. 94 (Pacific); Forster, 1844, pp. 198, 257 (Tahiti and New Hebrides); Gunther, 1861, p. 459 (New Ireland).

Mugil lauvergnii Eydoux and Souleyet, 1842, p. 174, pl. 4, fig. 3 (Macao); Gunther, 1861, p. 410 (Macao); Bleeker, 1873, p. 143; Chu, 1931, p. 104 (China).

Mugil heterocheilos Bleeker, 1855, p. 198; 1859, p. 278 (Batjan, East Indies); 1860*b*, p. 69 (Celebes); Gunther, 1861, p. 457; Weber, 1895, p. 268 (Australia); 1913, p. 142 (East Indies).

Mugil heterochilus Weber and de Beaufort, 1922, p. 258 (East Indies); Duncker and Mohr, 1926, p. 130 (New Pomerania and Admiralty Is.); Fowler, 1928, p. 126 (Oceania); Gunther, 1861, p. 457 (Batjan, Celebes; Ceram, Java).

Mugil ruppellii Gunther, 1861, p. 458.

Mugil crenilabris Kner, 1865, p. 229, pl. 9, fig. 4; Gunther, 1880, p. 69 (Pacific); Day, 1878, p. 355 (India); Streets, 1877, p. 93 (Hawaii).

Mugil neocaledonicus Castelnau, 1873, p. 116 (New Caledonia).

Querimana crenilabis Jordan and Seale, 1906, p. 218 (Samoa); Seale, 1906, p. 15 (Tahiti).

Liza crenilabis Kendall and Goldsborough, 1911, p. 258 (Pacific); McCulloch, 1929, p. 117 (Queensland).

Chelon crenilabis Oshima, 1922, p. 257, pl. 13, fig. 1 (Pescadores Is.).

Oedalechilus cirrhostomus Whitley, 1941, p. 19 (Lord Howe I.).

Type locality: Red Sea.

D.IV, I, 8; A.III, 9.

Scalation.—L1, 38-40, tr. 13-14; predorsal 20, cheek scales 3 rows. Scales cycloid, with an elongate straight mucous canal.

Body robust, deep, head length greater than depth in small specimens but less than the depth in specimens over 25 cm L.C.F.; dorsal profile almost straight, snout outline broadly rounded dorso-ventrally. Eye diameter greater than the snout length. Both lips thick, crenulated, and papillated, lower lip folded outwards, mouth cleft horizontal, not reaching to eye, no teeth, which are apparently represented by the papillae, teeth on palatines, and small patches on the tongue, but none on the vomers or pterygoids. End of maxilla hidden but slightly bent downwards; outline of mouth broadly angular, mandibulary angle broadly obtuse. Margin of operculum at pectoral base vertical. Preorbital, notched denticulations on ventral edge obsolescent, but more distinct on the narrow posterior side. Nostrils about equidistant from each other and the eye and upper lip.

The pectoral fin is almost as long as the head. It reaches the origin of the 1st dorsal fin and, turned forwards, it reaches in front of the eye. Axillary scale present. Ventrals shorter than the pectorals. Ventral obbasals very long, and longer than the interventral flange. The 1st dorsal fin originates at the 12th scale, and has a long obbasal which reaches behind the base of the 4th spine. The 2nd dorsal origin is at the 23rd or 24th scale behind the origin of the anal fin, which is higher than the 2nd dorsal, which is higher than the 1st dorsal; fins only slightly scaled anteriorly. Second dorsal and anal fins fairly deeply emarginate; the caudal only slightly.

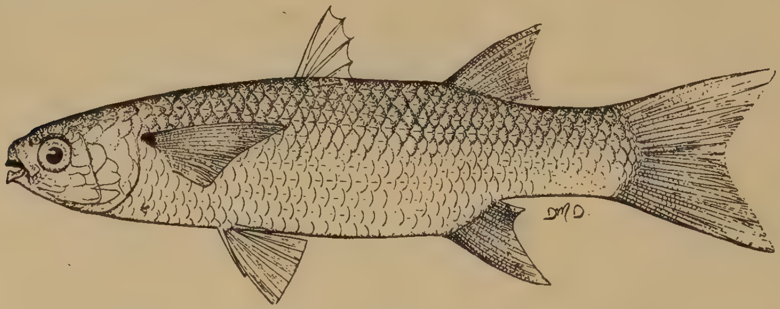

Fig. 13.—*Crenimugil crenilabis* (after Smith 1949).

Gill-rakers: 50/60.

Length.—At least to 40 cm L.C.F.

Coloration.—Upper olive-green, silvery on sides, and ventrally fins greyish, except pectoral, which is pale yellow with a purple axillary spot.

Discussion.—Whitley (1941) distinguished *cirrhostomus* from *crenilabis* on scale count; but examination of his specimen of *cirrhostomus* (Australian Museum I 4081, a very small specimen) reveals not 35 lateral scales but 37, which Fowler (1939*b*) attributed to *crenilabis*. The proportional differences mentioned by Whitley are all subject to alteration with age and his specimen is small—only 92 mm L.C.F. Whitley's (1927*a*) specimens of *crenilabis*, which he placed in the synonymy of his (1941) *cirrhostomus*, have 39-40 lateral scales.

Material.—Australian Museum: I 4081 (Lord Howe I.); I 6574 (Santo, New Hebrides); IA 2693 (Michaelmas, Queensland); IA 2841; IA 2864 (Vanikoro lagoon); IA 5526 (Ellice Is.); IB 1513 (Purdy Archipelago; New Guinea).

15. CRENIMUGIL LABIOSUS (Cuvier & Valenciennes)

Fig. 14

Mugil labiosus Cuvier and Valenciennes, 1836, p. 93 (Red Sea); Bleeker, 1854, p. 213 (Sumatra); 1859, p. 278 (East Indies); 1860*a*, p. 33 (Borneo); Gunther, 1861, p. 454 (Timor, Red Sea); Day, 1878, p. 346 (India); Klunzinger, 1870, p. 826; 1884, p. 133 (Red Sea); Weber, 1913, p. 140; Weber and de Beaufort, 1922, p. 260 (East Indies); Duncker and Mohr, 1926, p. 130 (Pacific); Fowler, 1928, p. 126; 1934, p. 309 (Oceania); Giltay, 1933, p. 115 (East Indies).

Mugil cirrhostoma Gunther, 1861, p. 459 (New Ireland).

Mugil papillosus Macleay, 1883, p. 270 (Normanby I., New Guinea); Tosh, 1903, p. 19, pl. II, fig. 3.

Liza papillosa Jordan and Seale, 1906, p. 218 (Samoa); McCulloch, 1929, p. 117 (New Guinea).

Oedalechilus papillosus Whitley, 1941, p. 20, fig. 15 (Normanby I.).

Type locality: Red Sea.

Vernacular name: fringe-lipped mullet.

D.IV, I, 8; A.III, 9.

Scalation.—L1, 34-36; tr. 11-12; predorsal 20; cheek-scales 3; scales cycloid with an elongate straight mucous canal.

Body robust, dorsal profile convex, snout outline slightly pointed. Head length less than body depth; eye diameter greater than the snout length. Upper lip thick, high, slightly crenulated and with a few rows of papillae, lower lip without papillae or a few obsolescent ones laterally; symphysial knob high and feebly double. No teeth on palate, a few on tongue, mouth outline broadly rounded; mandibulary angle obtuse. Margin of operculum vertical. Preorbital notched denticulate on posterior edge, ventral edge with denticulations obsolescent or absent. Nostrils about equidistant from each other and from the eye and edge of upper lip.

The pectoral fin reaches the 10th or 11th scale, not quite to the origin of the 1st dorsal fin, when turned forwards reaches in front of the eye. The pectoral base is short relative to the length. Small axillary scale present. The ventrals somewhat shorter than the pectoral but not so markedly as in *C. crenilabis*. The ventral obbasal and the interventral flange are quite short and of equal length. The 1st dorsal fin originates at the 11th or 12th scale, about midway between snout and caudal base. The dorsal obbasal is elongate, reaching well behind the base of the 4th spine. The 2nd dorsal origin is at the 23rd or 24th scale behind the origin of the anal fin, which is slightly lower than the 2nd dorsal but higher than the 1st dorsal. The anal, 2nd dorsal, and caudal fins are scaly basally and anteriorly and moderately emarginate.

Length.—Reaches at least to 28 cm L.C.F.

Coloration.—Olive-brown above, silvery on sides and below. Purple axillary spot.

Discussion.—There would appear to be some confusion on the identities of the species *labiosus, heterocheilos, papillosus,* and *cirrhosto-*

mus. The original descriptions are somewhat vague on important points. Whitley (1941) placed *heterochilus* Weber and de Beaufort in the synonyms of *papillosus,* and queried whether *heterocheilos* Bleeker was the same species; the last name having priority if it should be. But *heterochilus* Weber and de Beaufort has 41 lateral scales, whereas *papillosus* has 35. On the other hand *crenilabis* Forskal has 38-41 lateral scales; and *labiosus* Cuvier and Valenciennes has 34-36. I therefore assign *heterocheilos* to *crenilabis* and *papillosus* to *labiosus.* Both *papillosus* and *labiosus* are said to have no papillae or crenulations (Whitley 1941; Weber and de Beaufort 1922). Of the 3 type specimens of *papillosus,* the lectotype accords with this description but the other 2 show a few crenulations and obsolescent papillae on the lower lips.

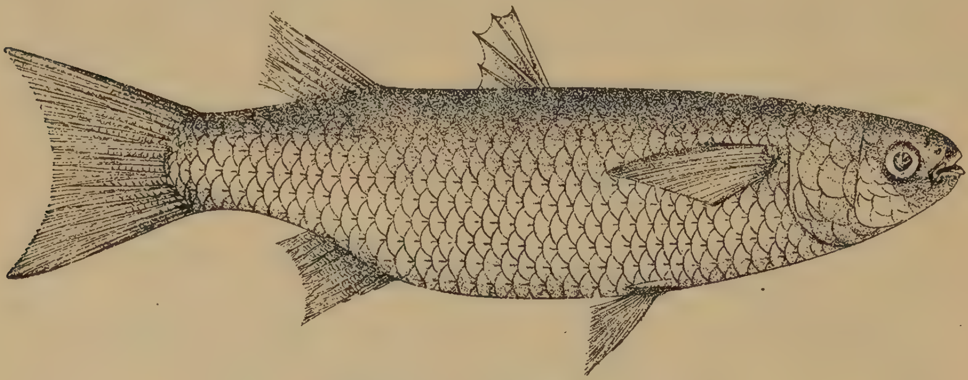

Fig. 14.—*Crenimugil labiosus* (after Tosh 1903).

Material.—I 13392 (lectotype of *papillosus*); I 13393-4 (cotypes).

16. CESTRAEUS GOLDIEI (Macleay)

Fig. 15

Aeschrichthys goldiei Macleay, 1884*a*, p. 5, text-figs, plate (Goldie R., New Guinea); Jordan and Seale, 1906, p. 218 (Samoa); Jordan and Richardson, 1908, p. 244 (Philippines); Weber and de Beaufort, 1912, p. 135 (East Indies).

Cestraeus goldiei Weber and de Beaufort, 1915, p. 26, fig. 2 (New Caledonia); Fowler, 1928, p. 128; 1934, p. 309 (Oceania); Schultz, 1946, p. 382 (New Guinea). .

Agonostomus goldiei Weber and de Beaufort, 1922, p. 262, figs. 68, 69 (Timor; New Guinea; Philippines).

Type locality: Goldie R., New Guinea (Type specimen Australian Museum).

Vernacular name: Goldie River mullet.

D.IV, I, 8; A.III, 9; P.I, 15-16.

Scalation.—L1, 37-39 tr. 13-14, predorsal 22; cheek scales 3 rows; scales ctenoid.

Body robust, profiles convex, head outline pointed in both dorsoventral and lateral outlines. Head short, less than depth. Snout length greater than eye diameter. Upper lip rather thick but not very deep; deepest centrally, upper tip terminal, overhanging lower lip, continuous with dorsal outline of head, not vertical, premaxilla and maxilla not bent downwards, reaching back under the eye. Maxilla hidden; a pair of fleshy lobes at the posterior end of the lips. Lower lip thickened with a narrow strip of very close-set transverse lamellae, ending posteriorly with 1 or 2 pairs of fleshy lobes. A row of simple-tipped setiform teeth on the upper jaw, a few scattered ciliform teeth on the lower lip becoming scarcer or absent with age. Teeth on vomers but none on palatines, pterygoids, or tongue. Mouth outline pointed angular, mandibulary angle acute. Gular space elongate and narrow. Nostrils close together below level of top of the eye, the posterior nostril large oval; the anterior small and pore-like. Adipose eyelid obsolescent, present as a rim around eye and in an anterior patch reaching to the posterior nostril and a posterior reaching a somewhat greater distance behind the eye. Head width narrow. Margin of the operculum slightly oblique at pectoral level. The preorbital is not notched but projects under the eye almost to the iris; denticulations on the wide posterior edge of the preorbital distinct, but obsolescent on the elongate ventral edge.

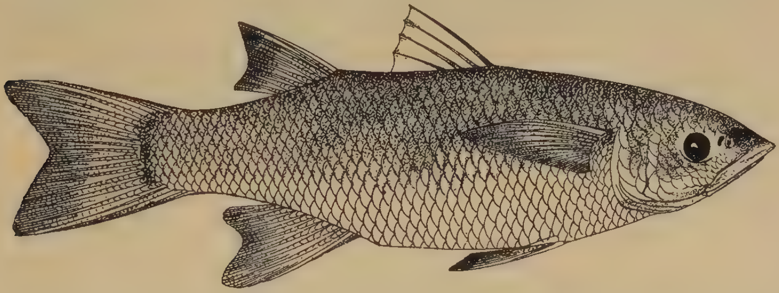

Fig. 15.—*Cestraeus goldiei* (after Weber and de Beaufort 1922).

The pectoral fin reaches the 1st dorsal origin at the 12th or 13th scale and turned forwards reaches in front of the eye. The axillary scale is of moderate length. The obbasals are shorter than the interventral flange. The 1st dorsal origin about midway between snout and caudal base. The 2nd dorsal originates at the 22nd or 23rd scale, behind the origin of the anal fin. The anal is higher than the 2nd dorsal, which is higher than the 1st dorsal. The 2 former and the anal are scaly and deeply emarginate.

Size.—Attains at least 40 cm L.C.F.

Discussion.—Teeth have been reported previously only in the upper jaw. But several of the specimens viewed had a few well-spaced ciliform teeth on the lower jaw. The smallest specimen seen measured 18 cm L.C.F., so that it is possible that such teeth are more abundant in younger fish. Schultz (1946) said, "apparently no teeth on vomer . . .", but Macleay's original description of teeth on these bases is correct. Weber and de Beaufort (1922) reported 2 series of teeth in the upper jaw. But Schultz mentioned "a row of setiform teeth"; and only 1 row appears to be present.

Material.—Australian Museum: I 9050-53; I 9060-61; I 9745; I 9747; I 13395-96 (Goldie R., New Guinea).

17. RHINOMUGIL NASUTUS (De Vis)

Fig. 16

Mugil nasutus De Vis, 1883, p. 621 (Cardwell, Rockingham Bay, Queensland); Macleay, 1885, p. 52 (Rockingham Bay).

Squalomugil nasutus Ogilby, 1908, pp. 3, 28; McCulloch and Whitley, 1925, p. 141 (Rockingham Bay); 1929, p. 96 (Adam Bay, Northern Territory); McCulloch, 1929, p. 117 (Rockingham Bay, Adam Bay); Whitley, 1941, p. 22, fig. 16.

Type locality: Cardwell, Rockingham Bay, Queensland.

Vernacular names: shark mullet, mud mullet.

D.IV, I, 7; A.III, 8.

Scalation.—L1, 34 (+5) tr. 11. Predorsal 17, cheek scales 2 rows, scales cycloid and on belly feebly ctenoid with a long straight mucous canal.

Body slender, head flattened, concave between the eyes, which project above the head level. Snout terminal, overhanging the lips. Body deepens suddenly behind the head. Head length greater than body depth. Snout length slightly less than eye diameter. Upper lip thin, maxilla straight, not exposed; mouth cleft slightly oblique; lower lip thin with a low symphysial knob; a few fine scattered spatulate teeth on jaws, no teeth on palate or tongue. Maxilla hidden, mouth not protrusible, mouth outline angular, mandibles obtuse. Nostrils widely separated; anterior nostril level with lower $\frac{1}{3}$ of eye. Posterior nostril $\frac{1}{3}$ of way from upper edge. Both nostrils pore-like, the posterior rather bigger than the anterior. Head very wide posteriorly, but narrowing sharply to be very narrow interorbitally. Adipose eyelid obsolescent, present as a rim projecting very slightly onto the eye, and about eye. Margin of the operculum markedly oblique at the pectoral level, with a triangular projection backwards over the base of the pectoral fin. The preorbital not notched, narrow, coming to a point posteriorly, posterior edge obliterated, anterior edge denticulate.

The pectoral fin is almost as long as the head, its origin a distinct distance behind operculum edge; it reaches to the origin of the 1st dorsal fin at the 10th or 11th scale; turned forwards just reaches in front of the eye. The axillary scale is short and widely triangular. The ventrals, about $\frac{2}{3}$ as long as the pectorals, originate well back from the head; and the ventral spine reaches the level of the origin of the 1st dorsal. The obbasals are of moderate length and shorter than the interventral flange. The 1st dorsal origin is nearer the base of the caudal than to the snout. The dorsal obbasal is longish. The 2nd dorsal origin is at the 20th or 21st scale, more than $\frac{1}{2}$ way along the anal base. The 2nd dorsal and anal fins are quite high and equal in height; the 1st dorsal is considerably lower and is short based. The 2nd dorsal and anal fins are somewhat scaly anteriorly. The unpaired fins are only very slightly emarginate.

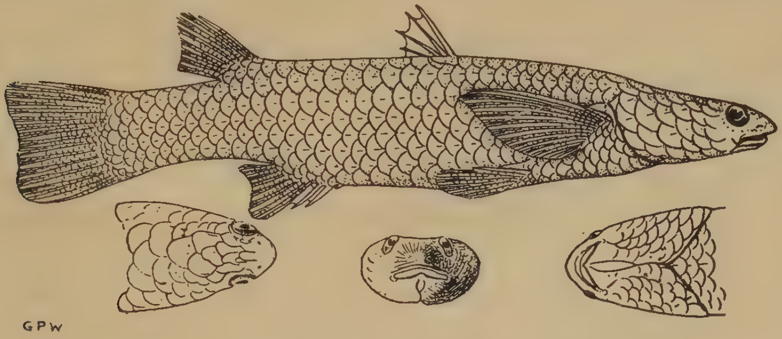

Fig. 16.—*Rhinomugil nasutus* (after Whitley 1941).

Length.—At least to 32 cm L.C.F.

Discussion.—Whitley (1941) said there are no true teeth. There are in fact on both jaws scattered fine spatulate teeth visible only under a lens.

Material.—Australian Museum: I 12693 (cotype) (Cardwell, Queensland); IB 1751-4 (Mackenzie I., Queensland); IA 3066 (Adams Bay, Northern Territory). Harbours and Marine Museum, Brisbane: 619-20 (Princess Charlotte Bay, Queensland).

V. ACKNOWLEDGMENTS

Dr. A. B. Walkom, Director of the Australian Museum, Sydney; Mr. H. Longman, when Director of the Queensland Museum; and Mr. L. Glauert, Curator of the Perth Museum, are thanked for permission to work on the collections in their institutions. Mr. G. P. Whitley, Curator of Fishes, Australian Museum, was extremely helpful in suggestions of possible synonymy and in general discussions. Dr. J. L. B. Smith kindly sent specimens of South African fish. The Institute of Oceanography, Monaco, sent specimens of Mediterranean mullet. Dr. T. Abe of the Department of Zoology, Tokyo University, gave access to the collection of that institution; Dr. K. Kurunuma and other Officers of the Japanese Central Fisheries Organization provided fresh specimens of Japanese mullet. The author is deeply indebted to Mr. I. S. R. Munro for the original drawings of Figures 1-5.

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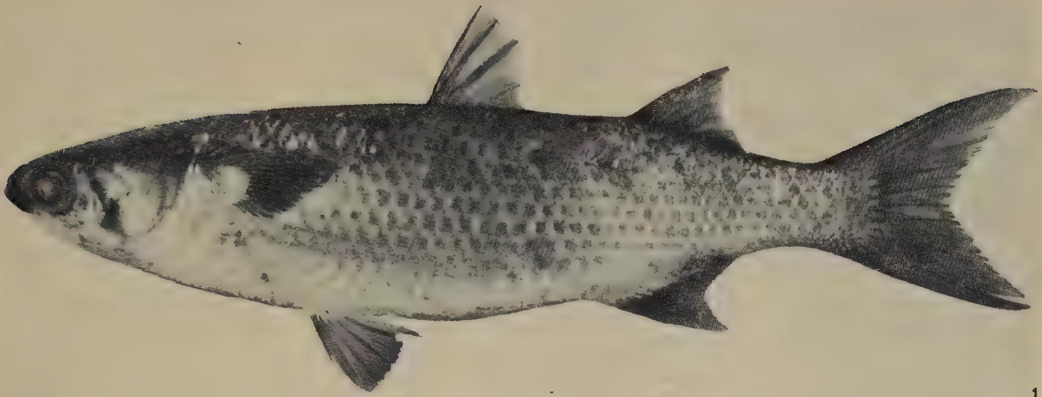
MUGILIDAE OF AUSTRALIA



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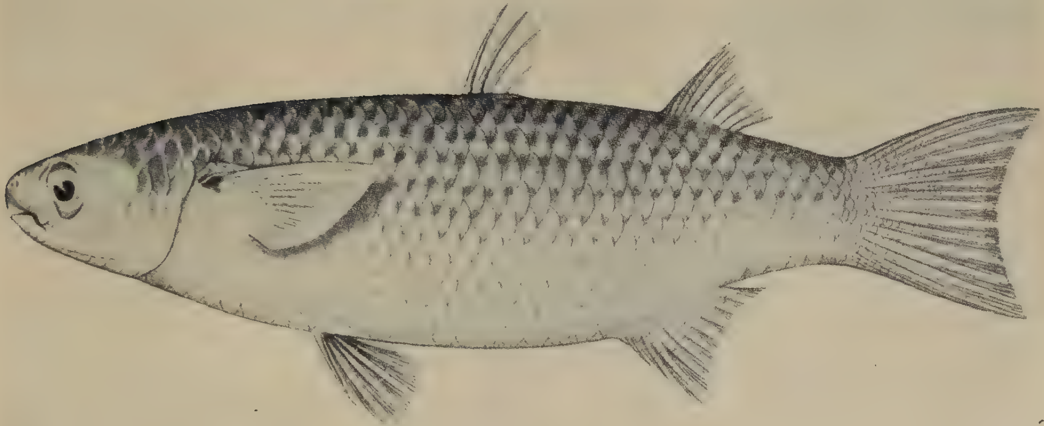

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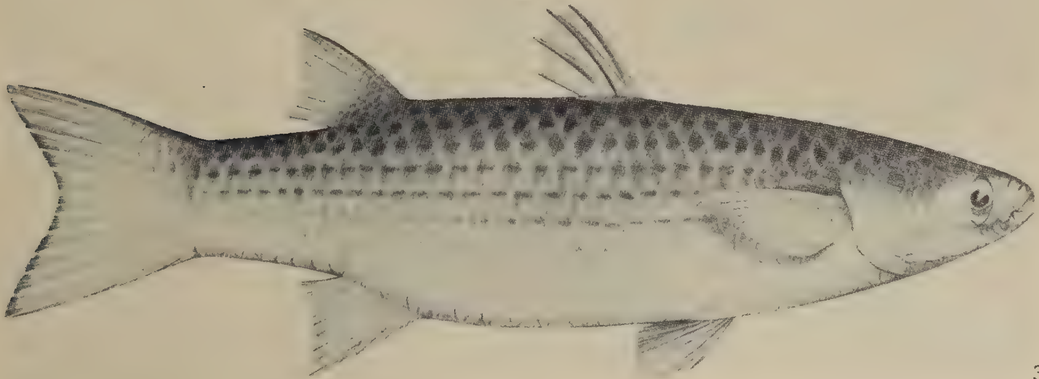

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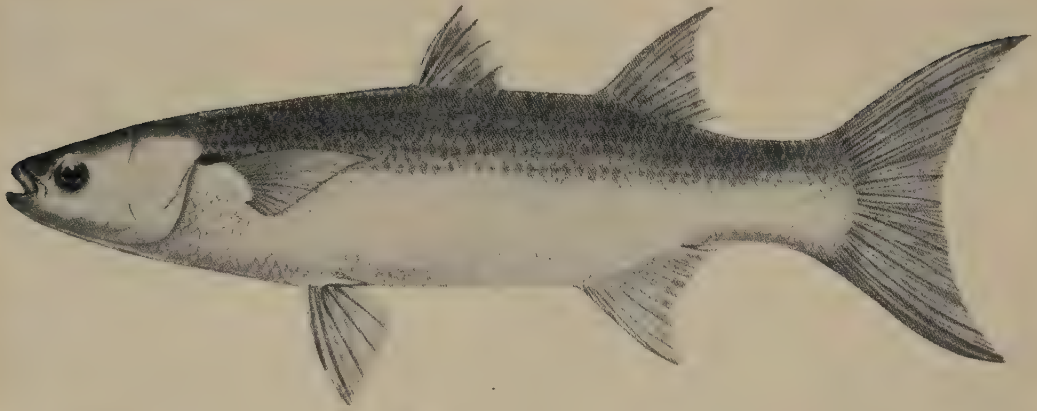
Fig. 1.—*Mugil cephalus.*
Fig. 2.—*M. georgii* (after McCulloch 1921).
Fig. 3.—*Liza dussumieri* (after McCulloch 1921).



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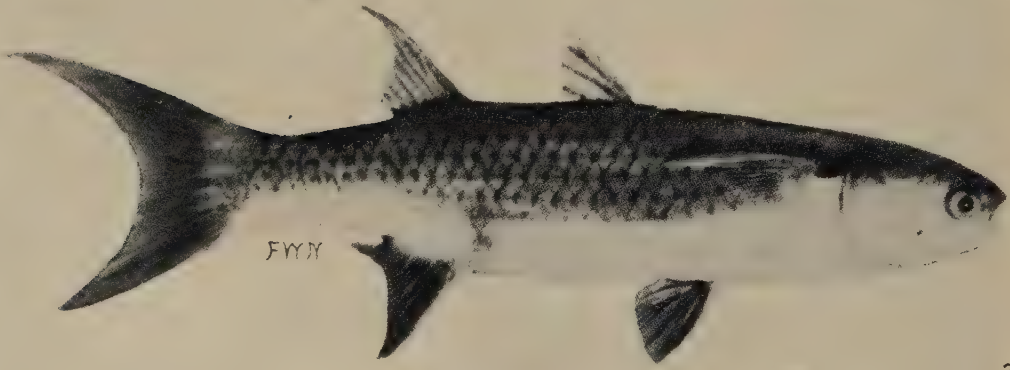

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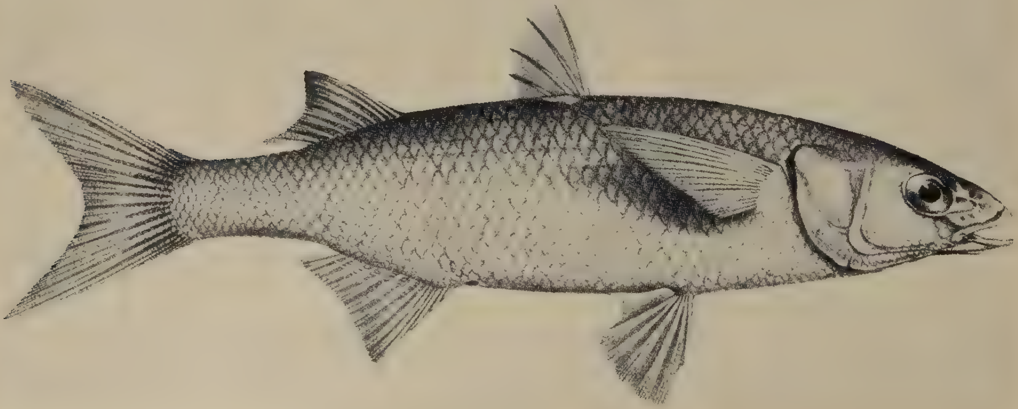

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Fig. 1.—*Valamugil seheli* (after Marshall 1951).
Fig. 2.—*V. buchanani* (after Smith 1949).
Fig. 3.—*Aldrichetta forsteri* (after Richardson 1845).

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THE GENERA OF OYSTERS AND THE AUSTRALIAN SPECIES

By J. M. Thomson*

(*Manuscript received November 30, 1953*)

Summary

Both conchological and malacological characters have been applied to the differentiation of the genera and species. Characters not previously used include the arrangement of tentacles on the mantle folds and the pigmentation on gills, palps, and mantle folds. Three genera are recognized, *Ostrea* Linnaeus, *Crassostrea* Sacco, and *Pycnodonte* Fischer de Waldheim. Ten native species of Australian oyster and one imported species are described in detail. Two keys to the species are provided, one based on shell characters and one based on the details of the soft anatomy.

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I. Introduction

The basis of previous determinations of the species of Australian oysters, notably by Cox (1883), Saville-Kent (1893), and by Iredale (1939), has been entirely conchological. Recently the author was enabled to study the anatomy of the soft parts as well as the conchological characters of a large series of Australian oysters. In view of the notoriously variable conchological characters of oysters (Bell 1921; Orton and Awati 1926; Nelson 1938; Ranson 1943) and in view of recent nomenclatural and taxonomic reviews of the Ostreidae by MacLean (1941), Ranson (1943, 1948*a*), Stenzel (1947), and Gunter (1950) it is considered desirable to review the status and nomenclature of the Australian ostreids.

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* Division of Fisheries, C.S.I.R.O., Cronulla, N.S.W.

II. TAXONOMIC CHARACTERS

(*a*) *Conchological Characters*

Although Ranson (1943) deplored the use of all conchological characters except those of the prodissoconch, there are, as Gunter (1950) realized, certain shell characters that are generally constant, although shells which have suffered extreme distortion may be difficult to assign to the species or even the genus.

Ecomorphic forms are produced according to the exact niche occupied by the individual. Exposure to surf or heavy wash results in thicker, heavier shells, the sculpturing is bolder, both the radial folds and the crenulations of the lip being much more definite than in specimens of the same species from sheltered situations; the marginal denticles are better developed, and the young shells may produce spinous processes.

Prolonged exposure to direct sunlight and exposure of normally estuarine species to highly saline water results in stunted forms, distinguished by bleaching and by the crowded growth fringes.

Permanently submerged specimens of the genus *Crassostrea* have a more deeply cupped lower valve than intertidal forms of the same species. Oysters growing on mud or on shifting sand develop imbricate frills during the struggle to keep above the soft or moving substrate.

Shallower and more recumbent oysters are found on flat surfaces and such oysters frequently have thin papery shells against the substrate. Adherence to narrow or curving surfaces may be achieved in a few species by the formation of tube-legs which may be marginal props or axial claspers according to circumstances. Severe distortion may occur in overcrowded situations or in oysters which happen to have settled in the cracks of rocks or other positions where normal growth is impossible owing to limitations of space. Semitubular shells are formed by some species when overcrowding occurs.

(i) *Cavity of the Valves.*—A distinction of generic usefulness lies in the nature of the cavity of the lower valve. This may be deep and cup-shaped with a recess of greater or less extent below the hinge (such shells are designated as "cucullated" by some authorities), or it may be quite shallow and lacking the recess. The upper valve may be almost straight and opercular or curved and hollowed to various degrees. The cavity of the upper valve is usually markedly less than that of the lower valve but it is subequal in the genus *Pycnodonte*. The upper valve may be domed near the hinge to accommodate the visceral portion of the oyster's body.

(ii) *Structure of the Shell.*—Korringa has recently (1951) described the layers of the shell typical of the genus *Ostrea*. Amongst Australian members of the genus only *O. angasi* Sowerby has the scaly prismatic layer well developed. In the other species and in the genus *Crassostrea* this layer rapidly wears off.

The lower valve is usually more massive than the upper, even when the cavities are subequal. The shell of the genus *Pycnodonte* is peculiarly vacuolated (Ranson 1941).

The valves are strengthened by folds of greater or less prominence which end in the crenulations of the rim. These folds are termed ribs, ridges, or flutings by various authors, and some apply the terms differentially according to the prominence of the fold. However, as an infinite gradation occurs it is considered better to use the one term, folds. Some species constantly have about the same number of folds (e.g. *Crassostrea amasa* Iredale), but it is not invariable and some species, such as *Ostrea folium* (Linnaeus), show marked individual and ecomorphic differences in the number and prominence of the folds. The folds of the lower valve may be obsolescent when the oyster is broadly adherent. The crenulations of the rim may be roundly curved, termed here "broadly crenulated", or sharply angled, here termed "sharply crenulated".

Within small limits of variation the hinge line is of uniform width, proportional to the size of the shell, for any species. Exceptional specimens of normally wide-hinged species may be narrow-hinged owing to the stress of environment, such as the restriction in a narrow crack or amongst an overcrowded clump of oysters, but a normally narrow-hinged oyster never becomes broad-hinged. The hinge plate itself may be quite short as is usual in species of *Ostrea*, or it may be long to cover the recess below the hinge in species of *Crassostrea*. The hinge ligament may be a narrow band, or it may have an expanded central portion.

The "beaks", that is, the portion of the shell anterior to the hinge, are useful generically, the beak of the lower valve of *Crassostrea* frequently being prolonged; but this feature is variable and not to be relied upon.

Small raised white teeth or denticles are formed around the internal edges of the upper valves of some species. They fit into matching grooves on the lower valve. They may be limited to a small strip on each side of the hinge or they may extend right around the rim. *Pycnodonte* differs in having elongate semitubular denticles on both valves. This genus also has on either side of the hinge triangular patches of irregular folds. Except in *Pycnodonte* the denticles have no generic value, as they are present or absent in various species of each of the other genera. Ranson (1948*a*) considered that denticles are more typical of *Ostrea* than of *Crassostrea* as he found denticles in only three of 20 species of the latter genus. But they are present in five out of six Australian species of the genus.

The prodissoconch characters have been described fully by Ranson (1948*a*) who showed their value in generic distinctions. Confirmation has been possible in only two Australian species, namely *Ostrea angasi* Sowerby and *Crassostrea commercialis* (Iredale & Roughley). Specimens of incubatory oysters with prodissoconch larvae were not available and although several oyster larvae are discernible in the plankton samples from tropical waters it is impossible to determine the species. Ranson (1948*a*) claimed that it is possible to detect details of the larval shells in the adult. But in all the specimens examined during this investigation sufficient weathering of the umbo had occurred to obliterate the details of the prodissoconch.

No pallial line is found in ostreids. The position and outline of the adductor muscle scar may have both generic and specific importance. In *Ostrea* the scar is more or less central, displaced only slightly to the dorsal side and distant by more than its own width from the lip end of the shell. But in *Crassostrea* both dorsal and posterior displacements are marked. The degree of displacement varies according to the species. The *Pycnodonte* spp. have a central muscle scar which in old specimens is raised on an oblique ledge or platform.

The outline of the scar is generally circular in *Pycnodonte,* but in the other genera it is straight or lunately excavated along the border towards the hinge.

(iii) *Coloration.*—The external coloration includes a simple ground colour, usually white, off-white, yellow, or purple, which may be suffused or splotched by other pigmentation or it may be marked by streaks of variable width passing interruptedly from hinge to lip. Erosion or bleaching may obscure the pigmentation of old specimens. For each species there is a range of pigment patterns and a range of shades of colour from which specimens do not vary, though they may overlap the range of another species. For instance, *Ostrea folium* Linnaeus is generally bronze-red but some specimens are purple, simulating the coloration of *O. trapezina* Lamarck. This latter species is normally purple, never bronze, though sometimes pale brown, and other specimens range to a greenish hue. Iredale (1939) attempted to use coloration as a generic character but this is not valid.

The internal coloration is usually white, off-white, or greenish and is specifically constant. There may be streaks of other pigments, principally purple or blue, but these should be distinguished from such foreign inclusions as mud blisters which occur, more particularly in estuarine forms. The scar of the adductor muscle is sometimes similar to the rest of the internal coloration, but it may be streaked, splotched, or entirely filled in by another colour, usually purple, black, blue, green, or even yellow. There is only one colour or range of a few shades characteristic of each species. The internal colours are usually dull but some species have an opalescent sheen. Occasional patches of chalky white shell are due to physiological processes explained by Korringa (1951) and have no taxonomic significance.

(*b*) *Malacalogical Characters*

The soft anatomy of the oyster is not very variable; doubtless there are microscopical differences, such as the size of the ostia, already elucidated by Elsey (1935) but the malacalogical characters of taxonomic usefulness are limited and have been almost entirely ignored by most systematists.

(i) *The Promyal Chamber.*—The presence of a promyal chamber clearly distinguishes one group of oysters from the rest (Nelson 1938). It has been confirmed that all the Australian species here referred to *Crassostrea* possess a promyal chamber.

(ii) *The Gill Ostia.*—Elsey (1935) indicated that incubatory species of oyster had comparatively large gill ostia and the non-incubatory types had small ostia. This is of generic importance.

(iii) *The Gill Plicae.*—The numbers of gill bars to a plica in the central portion of the gills is fairly uniformly 12-14 but some species have fewer. The gill bars and the gill edge are pigmented in some species. The gill bars are most certainly counted in sectioned material; but they can be counted externally on live material under low magnification, provided the gill is not obscured by detritus.

(iv) *The Pallio-branchial Fusion.*—Hirase (1930) has used this as a point of specific distinction but the exact position seems to vary according to the particular shape of the individual oyster and never to be very far from the one place. Constriction of the mantle may pull it out of its normal position in preserved or irritated specimens.

(v) *The Heart.*—Like most pelecypod hearts the ostreid auricles are double and the ventricle single. The auricles are joined (at least in the Australian species) either narrowly or widely, a distinction which appears to be generic. The tissue forming the heart is very flimsy and extreme care is needed to dissect it whole; sectioning can easily disrupt the membranes. This may explain why Hirase (1930) recorded some species having the auricles entirely separate, though this may yet be confirmed. The genus *Pycnodonte* is unique amongst the ostreids in having the ventricle penetrated by the rectum.

(vi) *Rectum and Anus.*—The rectum may be adherent to the adductor muscle for its entire distance along that organ, but in some species it is attached only near the anal end. The rectum may open at the anus either dorsally to the adductor or to a various extent beyond it. The amount of free portion of the rectum is a specifically useful character, and an extreme projection beyond the adductor is found in the genus *Pycnodonte.* The rectum is variously pigmented in different species and others have no pigmentation. The pigmentation may continue right to the anal opening, but others have a contrasting collar around the anus.

The anus itself is usually a compressed oval, but *Pycnodonte hyotis* (Linnaeus) has a ventral groove and adjacent to the groove on the upper side is a peculiar fold of the wall.

(vii) *Adductor Muscle.*—The adductor muscle is divisible into "catch" and "quick" muscle (Yonge 1936). The catch muscle area (adjacent to the hinge) includes more than 50 per cent. of the adductor in the genus *Ostrea* but usually only about 30 per cent. in *Crassostrea* and even less in *Pycnodonte.*

(viii) *Mantle.*—The mantle of some species can be thrown into radial ridges, particularly in the inhalent and exhalent areas; the depth of the grooves so formed varies specifically but some species seem to lack the ability to form them. The mantle edge has three folds (Elsey 1935; Nelson 1938) of which the inner two are pigmented and bear tentacles. The outermost fold has no tentacles and in most species is not pigmented. The relative size, spacing, and the pigmentation of the tentacles and the pigmentation of the inner and mid folds are diagnostic of the species. The tentacles of the inner fold are fringing and generally fairly short, being 2-3 times their basal width in length. In some species, for instance *Pycnodonte hyotis,* there may be little more than slight undulations of the mantle edge, as wide as they are long. The middle fold carries two rows of the tentacles, an outer marginal row of uniform length, except towards the hinge where all the tentacles become smaller; and an inner row usually considerably longer than the other rows, in most species projecting beyond the outer tentacles, and usually spaced so that several outer row tentacles fit between adjacent inner row tentacles. It is perhaps a misnomer to call this inner lot of tentacles a row. Their origins are not at a uniform height on the mid fold, but they spring from various points on the inner side of the fold, behind the marginal row, but they are uniformly longer than the outer row and clearly distinct from them. Hirase (1930) reported only two rows of tentacles in some of his Japanese species, but the possession of three rows is uniform throughout the Australian species of each genus. The smallness of some of the inner fold tentacles and the lack of pigmentation in these or in the outer row of the mid fold makes them very difficult to discern at times and careful turning of the mantle folds is necessary to detect them. Re-examination of the Japanese species is desirable, particularly as specimens of *Crassostrea gigas* imported into Australia from Japan (Thomson 1952) have proved to have the normal three rows of tentacles although Hirase records only two.

(*c*) *Physiological Characteristics*

The detailed physiology of oysters is largely unknown, and certainly is for comparative purposes. But some gross physiological data are known or inferred.

(i) *Spawning Habits.*—The oysters are clearly divisible into incubatory species (genus *Ostrea*) and non-incubatory (*Crassostrea* and *Pycnodonte*). Associated with this the number of eggs is less in incubatory oysters.

(ii) *Turbidity and Salinity Relationships.*—It has been frequently claimed that oysters with a promyal chamber (genus *Crassostrea*) are adapted for estuarine life, whereas those lacking it (*Ostrea, Pycnodonte*) are more suited to clear marine waters. A better and more generalized claim would be that promyal oysters are adapted to life in turbid waters, since some species occur far from estuaries, as along the Barrier Reef and Torres Strait Is., where, however, conditions are fairly turbid intertidally from the wash of the waves. It is true that species of *Ostrea* also occur in the same localities but very rarely intertidally where the wash of the waves stirs up the bottom. On the other hand *Ostrea angasi* does occur rather far up in the estuaries on the eastern Tasmanian coast and Western Australia, though these estuaries are drowned river valleys where the salinity is high and the waters clear except during the rainy season, which is rarely prolonged and seldom continuous.

(iii) *Depth Relationships.*—Oysters that commonly form intertidal reefs are almost without exception members of the genus *Crassostrea.* Members of the genera *Ostrea* and *Pycnodonte* are usually below low water mark, or at such a level that they only emerge at spring tides. Members of the *Crassostrea* group are equally at home below low water mark, as for instance on the dredge beds for *C. commercialis* in certain Australian estuaries and for *C. virginica* (Gmelin) on the eastern North American coast. Nevertheless there are certain species of *Crassostrea* which are seldom or never taken elsewhere than between tide marks, such as *C. amasa* and *C. echinata*; and others which almost never appear in that zone, such as *Pycnodonte hyotis.*

(*d*) *Dimensions and Axes*

In the prodissoconch the hinge is on the dorsal side of the animal, but after metamorphosis a reorientation of the body occurs (Stafford 1913; Cole 1938) so that in relation to the soft anatomy the hinge becomes antero-dorsal. The main axis of the body from mouth to anus runs from a point at the ventral end of the hinge to a point on the dorsal end of the lip (Fig. 1). Nevertheless, in speaking of the dimensions of the shell, the length will be taken from the hinge to the most distant part of the lip; the width will be measured as the widest part at right angles to this axis, and the depth will be the axis passing from one valve to the other where the other two axes cross. These are the dimensions as used by Thomson (1952) and, with slight modification, in that the depth was taken at the point of greatest depth, by Loosanoff and Namejko (1949).

The "lip", as used in this paper, means that part of the gaping edges of the shell on the side of the adductor muscle remote from the hinge, in general the part of greatest curvature of the shell rim.

To facilitate reference the terms upper and lower valves will be used rather than left and right. In all Australian oysters the lower attached valve is the left. Saville-Kent (1893) made a peculiar error in asserting that the commercial oyster, *Crassostrea commercialis,* is attached by the right valve.

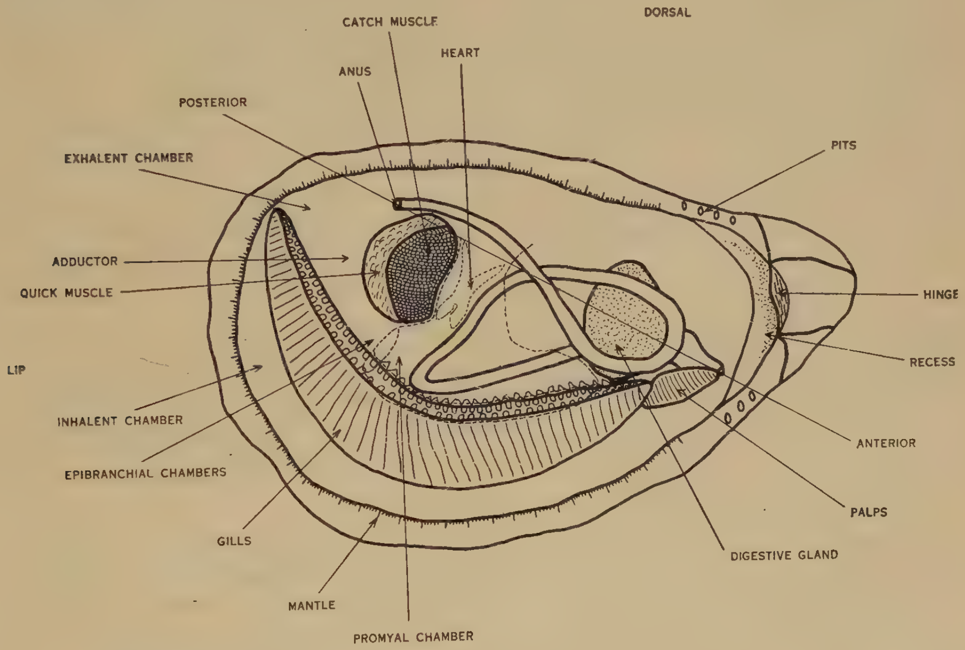
CATCH MUSCLE
DORSAL
HEART
ANUS
POSTERIOR
EXHALENT CHAMBER
PITS
ADDUCTOR
QUICK MUSCLE
HINGE
RECESS
LIP
INHALENT CHAMBER
ANTERIOR
EPIBRANCHIAL CHAMBERS
PALPS
GILLS
DIGESTIVE GLAND
MANTLE
PROMYAL CHAMBER

Fig. 1.—Dimensions and axes and points of reference in an oyster.

III. THE GENERA OF LIVING OYSTERS

The genera of oysters of the family Ostreidae have been reviewed in recent years by Stenzel (1947) on nomenclatural grounds, by Ranson (1943, 1948*a*) on biological grounds, and by Gunter (1950) from a more broadly taxonomic viewpoint.

Stenzel decided that there are 12 valid generic names but Gunter showed that several of these are not valid biologically and are synonyms of other names in Stenzel's list. Gunter allowed three definite genera, *Ostrea* Linnaeus, *Crassostrea* Sacco, and *Pycnodonte* Fischer de Waldheim; with three others of doubtful standing: *Dendostrea* Swainson; *Alectryonia* Fischer de Waldheim; and *Striostrea* Vialov. Ranson (1943, 1948*a*) admitted only three genera almost solely on the prodissoconch characters, merging all three of Gunter's doubtful genera in *Ostrea.*

Accumulating evidence on other features affirms the correctness of Ranson's grouping. However, there remains a doubt in nomenclature. Ranson (1943, 1948*a*, 1948*b*, 1949) recognized Lamarck's (1801) genus *Gryphaea* as valid instead of *Crassostrea* Sacco (1897), on the grounds that Children (1823) subsequently designated the living species *angulata* Lamarck as genotype. But Dall (1898), Hertlein (1933), Stenzel (1947), and Gunter (1950) have clearly shown that species *angulata* is not available for selection as the genotype of *Gryphaea* Lamarck (1801) as it is a nomen nudum with respect to that publication, being listed without indication, definition, or description. The subsequent validation of the species by Lamarck (1819) cannot make the name available for selection as genotype of *Gryphaea* Lamarck (1801). Ranson has argued that none of the 1801 species is valid as the published figures cited by Lamarck are not sufficiently well drawn to differentiate the species (at least in the opinion of Ranson). But many figures and descriptions, including many of Linnaeus and of Lamarck, do not serve to differentiate the species in the light of modern knowledge, though it has not been suggested that the many poorly defined species are invalidated on that account.

The references to Knorr and Bourget by Lamarck seem to be sufficient indication to validate the species referred to. If these species are accepted as valid as of 1801 then the genotype of *Gryphaea* is *G. arcuata* Lamarck by subsequent designation of Anton (1839); this being one of the six species listed by Lamarck which are clearly indicated by reference to previously published figures.

All the species of *Gryphaea* listed by Lamarck, other than *angulata*, are fossils of Jurassic and Cretaceous age, possessing peculiar conchological characters of which Lamarck thought he detected obsolescent traces in *angulata*. However Dall (1898) and Hertlein (1933) clearly indicate that *angulata* has no true generic relationship with the fossil *Gryphaea*.

The genotypes of the genera listed in the synonymy of the genera now to be defined are listed by Stenzel (1947) and by Ranson (1948*a*).

1. Genus OSTREA Linnaeus

Ostrea Linnaeus, 1758.
Lopha Bolten, 1798.
Alectryonia Fischer de Waldheim, 1807.
Dendostrea Swainson, 1835.
Ostreola Monterosato, 1884.
Alectryonella Sacco, 1897.
Eostrea von Ihering, 1907, partim.
Anodontrostrea Suter, 1917.
Euostrea Douville, 1920.
Monoeciostrea Orton, 1928.
Pretostrea Iredale, 1939.

Genotype (by subsequent designation, Schmidt (1818)): *Ostrea edulis* Linnaeus 1758.

Generic definition

Shell subcircular, relatively constant in shape within the species; lower valve shallow, not recessed under the hinge, muscle scar subcentral, upper valve may be flat and opercular, or domed and subequal to the lower, and it may or may not have denticles along the margin laterally to the hinge which fit into pits in the lower valve. Prodissoconch with a long hinge, 2 denticles at each end, of which the anterior pair are reduced; ligament at the centre or displaced slightly anteriorly. Without a promyal chamber, gill ostia and the eggs relatively large, fecundity relatively low; auricles of the heart unite broadly, the ventricle not penetrated by the rectum; "catch" area of the adductor muscle more than 50 per cent. of area. Incubatory forms. Habitat: usually totally submerged or baring only on spring tides, in highly saline waters free from turbidity.

Discussion

Ranson (1948*a*) united most of these synonymic genera under *Ostrea* on the features of the prodissoconch. Some of them are absolute synonyms. *Ostrea edulis* is the type of both *Euostrea* Douville and of *Monoeciostrea* Orton. *Ostrea crista-gilla* (Linnaeus) is the type of both *Lopha* Bolten and of *Alectryonia* Fischer de Waldheim.

According to Stenzel (1947) *Lopha* had no standing until 1898 when described by Dall, as Bolten published the name without definition, description, or indication. *Alectryonia* therefore takes precedence, but Ranson definitely and Gunter, with hesitation, assigned these to *Ostrea*. The only distinctive feature upon which these 2 genera were founded was the sharply crenulate nature of the shell margins, which is not a good distinguishing character, nor is that of *Dendostrea* Swainson, namely the axial claspers. As described below under *Ostrea folium* the author has found in this 1 species variants showing a range of characters which include those of *Ostrea folium* Linnaeus, *O. crista-galli* (Linnaeus), and *O. bresia* Iredale. Ranson (1943, 1948*a*) and Gunter (1950) have discussed the identity of *Alectryonella* Sacco.

2. Genus CRASSOSTREA Sacco

Crassostrea Sacco, 1897.
Gryphaea Lamarck, 1801, 1819, partim.
Euostrea Jaworski, 1913.
Dioeciostrea Orton, 1928.
?*Striostrea* Vialov, 1936.
Saxostrea Iredale, 1936.

Genotype: *Ostrea virginica* Gmelin.

Generic definition

Shell elongate, very variable shape even within the species; lower valve deep, cup-shaped, recessed under hinge; the muscle scar displaced both towards the dorso-lateral edge and towards the lip; upper valve opercular, flat except sometimes upraised at the rim, may or may not have a row of denticles along the rim laterally from the hinge. Prodissoconch with a short hinge, with 2 denticles at each end, the ligament anterior. A promyal chamber on the right side; gill ostia and eggs relatively small, fecundity high; auricles of the heart only narrowly joined; the "catch" area of the adductor forming less than 30 per cent. of the cross section. Non-incubatory types. Habitat estuarine or marine, usually but not necessarily intertidal, adapted to turbid water conditions and some at least to lowered salinities.

Discussion

Dioeciostrea Orton and *Euostrea* Jaworski are exact synonyms of *Crassostrea,* having *Ostrea virginica* Gmelin as their type. Ranson (1948*a*) is followed in attributing *Striostrea* to this genus. The original description of the type is not sufficient to determine whether it rightly belongs to *Ostrea* or *Crassostrea. Saxostrea* Iredale has absolutely no characters, either in description or in examination, to distinguish it from *Crassostrea.* Nelson (1938) recognized this when he allotted *commercialis* under the name *cucullata* to *Gryphaea.*

3. Genus PYCNODONTE Fischer de Waldheim

Pycnodonte Fischer de Waldheim, 1807.
Ostrea Linnaeus, 1758, partim.
Mytilus Linnaeus, 1758, partim.
Lopha Iredale, 1939, partim.
Pycnodonte Ranson, 1941.

Genotype: *Pycnodonte radiata* Fischer de Waldheim.

Generic definition

Large, ponderous, elongate shells, variable in outline; the lower valve moderately deep below hinge but not recessed to any marked degree; the muscle scar displaced dorso-ventrally and slightly towards the lip, peculiar in being elevated on a shelf-like projection; upper valve not as thick as the lower but the concavities of the 2 valves are subequal; both valves provided with elongate vermicular denticles; the edges and inner layers of the shell are peculiarly vacuolated. Prodissoconch hinge short, with 5 denticles along the hinge and 10 smaller ones anterior to the ligament, which is outside the cardinal plateau. With a promyal chamber on the right side; gill ostia and eggs small, fecundity high; auricles of the heart broadly joined; ventricle penetrated by the rectum; "catch" area of adductor very small; non-incubatory types; living totally submerged or at extreme low water in marine waters.

Discussion

Woodward (1880) included *Pycnodonte* in the synonymy of *Ostrea,* but it is clearly distinct, although superficially the shells are rather similar.

IV. THE AUSTRALIAN SPECIES

As hereafter defined there are 10 native Australian species and an imported species, which is included as it appears to be becoming acclimatized. Four of these species are assigned to the genus *Ostrea,* 6 to *Crassostrea,* and 1 to *Pycnodonte.* These species are clearly distinguished when all factors are considered. On shell characters alone it is sometimes difficult to distinguish some specimens from unusual habitat niches.

There has been a tendency for some Australian systematists, for example Iredale and Roughley (1933) and Iredale (1939) amongst conchologists, to distinguish Australian species from similar animals elsewhere for no other expressed reason than that they are Australian and the other species are recorded from somewhere else. While it may seem that such sedentary creatures as oysters could not spread very far, it must be remembered that the larval life may extend to 3 weeks. *Ostrea trapezina* extends from Moreton Bay in southern Queensland around the north of Australia at least to the North-west Cape area, W.A., and *O. angasi* is found along the coastline from south-western Australia to the Clarence River, N.S.W., and in Tasmania. The one species therefore can spread over a wide area and some of the islands to the north of Australia and westwards are not so far distant as these limits are from another, although it is true that shallow shores do not connect them continuously. From the prevailing current sweeps (Schott 1935) it is not impossible for the faunas of the East Indies, Australia, New Guinea, and the closer Pacific islands to be mutually influencing each other.

It is impossible to visit all the type localities of various species named from the Indo-Pacific and in the absence of live material of such oysters some nomenclatural problems remain. It is hoped that the observations on Australian oysters recorded here will stimulate workers elsewhere to observe the live material.

1. Genus OSTREA Linnaeus

OSTREA ANGASI Sowerby

Plate 1, Figs. 1-3

Ostrea angasi Sowerby, 1871, pl. XIII, fig. 28; Cox, 1883, p. 124; Iredale, 1936, p. 269; Lamy, 1929, p. 33.

Ostrea edulis Saville-Kent, 1894, pp. 179, 184; Tenison-Woods, 1878, p. 56.

Ostrea sinuata Cotton & Godfrey, 1938, p. 86, fig. 73; Allan, 1950, p. 273, text fig. 67, fig. 1.

Ostrea virescens Angas, 1867.

Ostrea rutipina Tenison-Woods, 1878, p. 56.

Vernacular names: mud oyster; Port Lincoln oyster; Stewart Island oyster.

Adherent when young, but generally free when an inch or two long. The shell is large and rounded in outline, being the most regular of the Australian oysters in shape. The space between the valves is shallow; in the larger specimens the lower valve becomes very massive, but in the younger specimens it is quite thin though dense; a few semicircular growth ridges are apparent and remote from the hinge the valve becomes very slightly fluted and indefinitely crenulated along the margin. The upper valve is almost flat except for a slightly domed portion near the hinge; the outer surface is ornamented with broad imbricate scales, forming the true prismatic layer of the shell (Korringa 1951).

The lower valve is greyish white externally; the upper is a similar colour near the hinge in older specimens where the prismatic layer has worn away, but more distally it is brown or dull purple in colour. Internally the valves are chalky white with a brown border. The muscle scar is white and broadly lunate in shape. There is a slightly upraised rim internally on both valves. Several denticles are present on either side of the hinge of the upper valve. These tend to disappear in older specimens. The ligament is purplish to brown.

The palps and gills are greenish grey in colour; the pallial-branchial fusion is well dorsal, reaching to the level of the lip end of the adductor muscle. The tentacles of the mantle folds are unusually broad and unusually closely set. The tentacles of the inner fold are broad, about ½ their basal width apart, and 3-4 times their basal width in length. They are heavily pigmented with brown. The tentacles of the middle fold have an off-white ground colour, which is heavily suffused with brown. The marginal row are small, only 1½-2 times their basal width in length, and ½ the basal width apart; the inner row of the middle fold are very plump, though not very long, being only 4 times their basal width. The tentacles of the inner row overlap, presenting a solid curtain of tentacles.

There is a broad band of brown pigment on the inner fold at the base of the inner tentacles. The outer groove is shallow but definite; the inner groove is deep and lightly coloured by brown pigment. The auricles of the heart are purplish red in colour and are broadly joined; 12-14 bars occur per plica of gill.

Range

Reported from Swan River, W.A., along the southern coast of Australia to Tasmania and north along the east coast to the Clarence R. It is not common anywhere, though small quantities are occasionally marketed in Tasmania and South Australia. Usually found in estuaries, but marine beds are also known.

Discussion

Cotton and Godfrey (1938), followed by Allan (1950), have attributed this Australian species to *Ostrea sinuata* Lamarck. But the type of specimen of *sinuata* in the Muséum Nationale d'Histoire Naturelle de Paris is a *Crassostrea* with a recess under the hinge and is quite possibly identical with *Ostrea plicatula* of Lamarck as indicated by Lamy (1929). It is a distorted shell but it is certainly not *O. angasi*. The name *angasi* was applied first to the New Zealand oyster. There does not seem any good reason based on the characters of the shell and the soft anatomy of the adults to separate the 2. There seems to be a greater proportion of dark-shelled oysters amongst the New Zealand examples but there are no other discernible differences. Ranson (personal communication) states that he finds differences in the larval stages, but pending the publication of his results it seems preferable to keep the 2 united.

OSTREA TRAPEZINA Lamarck

Plate 1, Fig. 4; Plate 2, Figs. 1, 2

Ostrea trapezina Lamarck, 1819, p. 206.
Ostrea imbricata Cox, 1883, p. 131 (non Lamarck, 1819).
Ostrea sellaformis Saville-Kent, 1891, p. 4, pl. 4, figs. 4, 5.
Ostrea sellaeformis Saville-Kent, 1893, p. 250, chrom.-pl. 16, fig. 6 (non Conrad, 1833).
Ostrea quirites Iredale, 1939, p. 396, pl. 7, fig. 3; Allan, 1950, p. 275.

Vernacular name: saddle oyster.

A subcircular adherent species. It may be closely adherent to a flat surface but often is adherent only adjacent to the hinge, and tubular projections from the lower valve help to support the shell on the substrate. The lower valve is shallow with a few indefinite folds ending in wavy indefinite crenulations at the lip. The upper valve is markedly convex, and in many older specimens, particularily when not closely adherent, is saddle-shaped. Several indefinite folds radiate to the lip, whose crenulations match those of the lower valve; the hinge line is moderately broad and the hinge plate narrow. The ligament is dark brown; the shell is greenish white with radiating narrow purple or sometimes red streaks (visible in Plate 2, Fig. 2), more particularly on the upper valve. The inside is opalescent white, sometimes with patches of chalky white, with a greenish border; muscle scar white, with a straight border on the hinge side. A few very small denticles, which often are visible only under slight magnification, occur on either side of the hinge. Young specimens frequently have short hollow tubular projections from the radiating ribs, which are more definite than in the adults.

The gills and palps are translucent white. The mantle is strongly ridged internally over a wide part of the incurrent and excurrent areas. The inner surfaces of the mantle folds are greenish white with a slight suffusion of brown pigment. The tentacles of the inner mantle fold are comparatively broad and dumpy, spaced ¼-½ their basal width apart, and 1½-2 times the basal width in length; they are translucent greenish white, fairly heavily suffused with dark brown pigment. The tentacles of the middle mantle fold are similarly coloured but with less dense suffusion of brown. The inner row of tentacles on the mid fold are only of moderate length (about 3-4 times their basal width); the outer row tentacles are about as long but not so broad as the tentacles of the inner fold and are spaced 2-4 between each tentacle of the inner row.

The auricles are very broadly united to each other and open widely into the ventricle. There are 12-14 bars per plica in the gill.

Dimensions

Grows to about 5 in. and is almost as broad as long; of shallow depth.

Range

From Moreton Bay along both mainland and the Barrier Reef to the Torres Straits and the Gulf of Carpentaria; it probably spreads along the entire northern Australian coastline as the species also occurs at North-west Cape and Shark Bay, W.A. Marine, almost always below low tide level.

Discussion

The type specimen of *Ostrea trapezina* Lamarck from Peron's collection in Shark Bay is this species, though it is abnormal in having almost rectangular corners to the lips, presumably due to compression while growing in a crowded position. In all other respects the shell is like the oyster named *quirites* by Iredale. *Ostrea sellaeformis* Conrad is a fossil and the name was misapplied by Saville-Kent.

OSTREA FOLIUM Linnaeus

Plate 2, Figs. 3, 4; Plate 3, Figs. 1-4

Ostrea folium Linnaeus, 1758, p. 534; Chemnitz, 1782, p. 665; Dillwyn, 1817, p. 274; Wood, 1828, p. 11, fig. 62; Lamarck, 1819, p. 200; Dunker, 1882, p. 249; Saville-Kent, 1891, p. 3; 1893, p. 244; Hirase, 1930, p. 21, figs. 35-37; Lamy, 1929, p. 2444.

Ostrea erucella Lamarck, 1819, p. 202.

Dendostrea folium Sowerby, 1839, p. 137, fig. 181; Swainson, 1840, p. 389; Gray, 1847, p. 201; Iredale, 1939, p. 402, pl. 7, fig. 11; Allan, 1950, p. 275, fig. 65, fig. 2.

Ostrea imbricata Cox, 1883, p. 131 (non Lamarck, 1819; Hirase, 1930).

Ostrea circumsuta Saville-Kent, 1893, p. 2.

Ostrea bresia Iredale, 1939, p. 396, pl. 7, fig. 4; Allan, 1950, p. 276.

Mytilus crista-galli Linnaeus, 1758, p. 704; Dillwyn, 1817, p. 299; Wood, 1828, p. 12, fig. 1.

Ostrea crista-galli Chemnitz, 1780, p. 683, fig. 4; Lamarck, 1819; G. B. Sowerby, 1875; Reeve, 1843, p. 121, fig. 2; Hirase, 1930, p. 19, figs. 31-34.

Ostrea cristagalli Cox, 1883, p. 131.

Lopha crista-galli Iredale, 939, p. 401; Allan, 1950, p. 273, pl. 30, fig. 19.

Vernacular names: bronze oyster, imbricated oyster, cox-comb oyster, leaf oyster.

Very variable conchologically; shell thin but strong; closely adherent to a flat surface but only slightly so on other surfaces, and with tubular attachment projections for attachment, which may be grouped near the edges or centrally. The lower valve is shallow, variably fluted with 4-8 folds, weakly so in totally immersed situations, but strongly in intertidal situations, weakly in closely adherent specimens, but more strongly the less the degree of adherence. According to the distinctness of the folds so the crenulations differ; adherent submerged specimens are only weakly crenulated but nearly always with a stronger crenulation in the postero-ventral corner of the lip. A complete gradation from this type to the scarcely adherent *crista-galli* type with strong crenulations may be found; the lower valve is shallow but has a somewhat upraised rim. The upper valve is shallow but slightly convex, with indistinct radial ribs which become distinct in the more crenulate specimens and often project as small tubes; the valve imbricate in some specimens, only obsolescently so in others. The hinge line is very narrow and the hinge plate is narrow, the ligament is brown centrally with a dark purple piece at each side. The external coloration is usually bronze-red, sometimes tinged with purple and rarely the purple predominates. In young specimens a central white streak passing along the upper valve from the umbo is quite typical (Plate 2, Fig. 3). Internally the colour is opalescent white with patches of green and purple, the muscle scar being white with similar tints and slightly excavated on the hinge side. Denticles are variably developed, but frequently extend more than $\frac{2}{3}$ of the distance around the edge, and frequently with a marked lateral space without any. The large sharp crenulations usually have teeth on 1 face only. The gills are pigmented in reddish bronze, and have 12-14 bars per plica. The tentacles of the inner fold of the mantle are short and broad, being only $1\frac{1}{2}$ times their basal width in length; they are spaced 2-3 times their basal width apart. The tentacles are pigmented bronze, as is the inner fold where occasional whitish streaks at right angles to the margin can be seen. The inner row of tentacles of the middle mantle fold are rather long (about 7 times their basal width) pigmented with bronze and having a large white patch near the base. The outer row of tentacles are small, about the same size as those of the inner fold, and are bronze or rich brown in colour. The mid fold itself is pigmented brown or bronze. The mantle is strongly grooved in the inhalent and exhalent areas. The rectum is closely adherent to the muscle, the anus being at the lip side of the muscle. The auricles are broadly joined.

Dimensions

Reaches about 3-4 in. in length; often as wide as long except for the *folium* type.

Distribution

From the Clarence R., N.S.W., to Torres Strait and the Gulf of Carpentaria, in submerged and intertidal situations, abundant submerged in marine waters of Indo-Pacific but also occurs on mangrove roots etc. in the lower estuaries.

Discussion

The typical subcircular bronze-red *bresia* is easily recognized as such. In these specimens the lip is indefinitely crenulated, but a complete range can be found from specimens with just wavy lips to sharply crenulate specimens. Three types are shown in the figures, a flat specimen closely adherent to a fibro-cement slab; a semi-adherent specimen which has developed supporting tubular projections at one side of the lower valve (the *crista-galli* type), and a 3rd with tubular projections from the centre of the lower valve clasping gorgonids and similar supports in typical *folium* manner. Although differing so widely in shape, particularly in crenulations, all these are bronze-red, all having a particularly sharp crenulation at the postero-ventral corner, all having denticles around the edge, interrupted at the mid-lateral portions; all are opalescent-white, with green and purple showing in patches internally; all have reddish bronze gills and mantle edge, with similar types of tentacle. The conclusion is inescapable that this is 1 species which responds variably according to the substrate and to degree of immersion. The forms recorded by Iredale (1939) and Allan (1950) as *Lopha cristagalli* and as *Dendostrea folium* from northern Australian waters are certainly only forms of this species. Iredale himself mentions that his *bresia* looked like a degenerate cox-comb oyster.

There remains the possibility that the Australian species is not identical with the *crista-galli* and *folium* of Linnaeus (1758). Certainly the *crista-galli* and *folium* of Hirase (1930) from the northern Pacific appear to be the same as their Australian counterparts. The only definite difference Hirase remarked in his 2 species was that the crenulations were smaller and more numerous in *folium.* This cannot be regarded as a valid ground for distinction. Hirase also states that he has taken *folium* adhering to seaweed by finger-like projections from the valve, but also adhering normally by the left valve. Woodring (1925) pointed out that specimens similar in every other respect to *Dendostrea* species were found without clasping arms. The *Ostrea cristagalli* of Cox (1883) is the more crenulate form of this species; while his *O. imbricata* is the more foliaceous, weakly crenulated form.

The shells named by Lamarck "*Ostrea folium*" have been examined by the author and are identical with the species as described here. The *crista-galli* of the same author, described from the same type area, differs only in the greater crenulations and the greater extent of the denticles. His *erucella* is a small *folium* with typical axial claspers.

It seems therefore that *Ostrea crista-galli* Linnaeus, *O. folium* Linnaeus, and *O. bresia* Iredale comprise the one polymorphic species. The first 2 names are of equal priority, but the trivial name *folium* has been selected both because of prior pagination and because it is intermediate in form between the other 2, at least as concerns the crenulations.

OSTREA NOMADES Iredale

Plate 4, Figs. 1-3

Ostrea crenulifera Saville-Kent, 1891, p. 3, pl. 12, figs. 5, 7 (non Sowerby, 1871).
Ostrea nomades Iredale, 1939, p. 395, pl. 17, fig. 1; Allan, 1950, p. 276.

Vernacular name: green oyster.

A small adherent species, recumbent. The lower valve is shallow, adherent by almost the whole surface, sharply upraised near the rim, with a few broad obsolescent folds on the upraised portion. The upper valve is greatly domed, folded only close to the edge where it meets the broad crenulations of the lower valve. The external colour is greenish white, occasionally dirty yellow; internally the colour is rather opalescent greenish white without any contrasting rim; the muscle scar pale green, dorsally displaced. Small denticles extend around most of the rim. Viewed from above the upper valve, there is a marked curve to the right from the umbo in most specimens.

The general mantle and gill coloration is greyish or greenish white. Even the mantle folds are usually without pigment though some specimens show pale brown pigments on the folds, and extending in a suffused way on to the tentacles. The tentacles of the inner mantle fold are small, about twice their basal width in length and 2-3 times their basal width apart, perhaps a bit closer in the incurrent and excurrent areas. The fringing tentacles on the mid fold are also short, about twice their basal width, about the basal width apart, and 5 or 6 between each inner row tentacle of the mid fold, the latter being rather longer, about 5 times their basal width in length, though not reaching far beyond the tips of the outer row tentacles. The rectum is unpigmented and reaches just to the lip side of the adductor muscle to which it adheres closely. The auricles are broadly joined and both are closely recumbent upon the ventricle. *O. virescens* Iredale (1936) and Allan (1950) is this species.

Dimensions

Reaching to about 2 in. in length, often broader than long.

Range

Port Jackson, Moreton Bay, Barrier Reef, Torres Strait, Gulf of Carpentaria; Iredale records specimens from the New Hebrides.

2. Genus CRASSOSTREA Sacco

CRASSOSTREA COMMERCIALIS (Iredale & Roughley)

Plate 4, Fig. 4; Plate 5, Figs. 1-3

Ostrea mordax Angas, 1867; Iredale, 1924, p. 192 (non Gould, 1850, p. 344).

Ostrea subtrigona Cox, 1883, p. 126 (non Sowerby, 1825).

Ostrea circumsuta Cox, 1883, p. 132 (non Sowerby, 1825).

Ostrea glomerata Cox, 1883, p. 132; Saville-Kent, 1891, pp. 1, 4, pl. 1, figs. 1-9; 1893, p. 243; chrom.-pl. 14, figs. 8-11; Iredale, 1924, p. 192; Roughley, 1928, (non Gould, 1850, p. 346).

Ostrea cucullata Hedley, 1909, p. 345; Roughley, 1926, p. 446; Boone, 1938, p. 324; Nelson, 1938, p. 57 (non Born, 1780, p. 122).

Ostrea commercialis Iredale & Roughley 1933, p. 278.

Saxostrea commercialis Iredale, 1939, p. 398, pl. 17, fig. 6; Allan, 1950, p. 273, pl. 30, fig. 15.

Vernacular names: Sydney rock oyster; mangrove oyster; rock oyster; commercial oyster.

An adherent species, markedly inequivalve, very variable in shape, the lower (left) valve deep and cup-shaped, and recessed under the hinge, moderately fluted, more strongly so in exposed positions; the edge of the valve weakly crenulate; the upper valve flattened, folded towards the lip to fit the crenulations of the lower valve. The hinge line moderately wide, though it may be short in specimens from crowded situations; the hinge plate moderate, the ligament blue-black in colour. The external coloration of the valves varies from bluish black to greyish white with indefinite blue-black borders, with intermediate forms showing 2 white rays crossing the black from hinge to lip on the upper valve. Internally the colour is chalky white, sometimes discoloured by foreign inclusions, with a bluish black or sometimes brown border which may be yellowish towards the hinges. The muscle scars are usually white but frequently have bluish or creamy markings, particularly on the upper valve. The muscle scar is displaced dorsally to within its own width of the lip and $\frac{1}{3}$ of its width from the dorso-lateral edge of the valve; the shape is broadly lunate with the recess on the hinge side. Small denticles are developed along the edge, close together adjacent to the hinge but further apart distally on the upper valve. These usually extend further on the ventral side, usually less than $\frac{1}{2}$ way around the valve but rarely to $\frac{2}{3}$ of the distance.

The gills and palps are cream in colour. The outer fold of the mantle is white but the middle and inner folds and the groove between are pigmented towards the edges. The tentacles on the inner fold are dark brown in colour, broadly based, about twice as long as the basal width, and about the basal width apart. The inner row of tentacles on the middle fold are long, about 6-8 times as long as their basal width generally, with 3 or 4 tentacles of the outer row between them in the incurrent and excurrent regions or 5-8 more laterally. They are translucent white suffused with fawn, dark brown, or black pigment. The outer row are relatively long compared with other species and project about ½ as far as the inner row. They are spaced 2-3 times their basal width apart and are translucent white with fawn patches. The groove between the outer and mid folds is not very deep but is distinct; that between the inner and mid folds is large. In the incurrent and excurrent regions the mantle is moderately grooved, the ridge being slightly pigmented a light tan with black specks. The remainder of the mantle is whitish except for a rim of brown around the inner fold which lightens in shade laterally. The gills are greyish and have 13-14 rods to a plica, the palps are creamy white with black tips in some specimens. The auricles of the heart are narrowly joined together.

Dimensions

Normally grows to 3-4 in., but carefully cultivated specimens have reached 10 in. from hinge to lip.

Range

From Wingan Inlet, Vic., to northern Queensland at least as far as Shoalwater Bay; mainly in the estuaries, but sometimes on rocky headlands and on various parts of the Great Barrier Reef; both intertidal and from dredge beds, widely cultivated in New South Wales and Queensland; attaches to rocks, sticks, and shell.

Discussion

A much elongated form has been figured by Iredale (1939) and by Boone (1938); these came from dredge beds and apparently are produced by the oysters' desperate attempts to grow above encroaching sand or mud. The author has noted similar elongate forms amongst sanded-over *Crassostrea gigas* (Thunberg) imported into Tasmania. Boone is in error in attributing *Ostrea mordax* var. *cornucopiae-formis* to *commercialis*. The elongate forms of *commercialis* have subequal valves whereas Saville-Kent's elongate specimens were the hooded or tube oysters referred by Allan (1950) to *Crassostrea scyphophilla*. Boone is also in error in stating that the type of Born's *Ostrea cucullata* came from Australia. It was recorded from material from Ascension I. and the West Indies (Roughley 1928; Iredale and Roughley 1933). The use of the name *cucullata* for Indo-Pacific forms is probably incorrect, and certainly *commercialis* differs distinctly from the Indian *O. cucullata* described by Awati and Rai (1931) and by Hornell (1917).

Cox (1883) considered the dredge oysters a separate species from the intertidal forms, but they are clearly the same, the difference in form being only ecomorphic. *O. glomerata* of Gould was described from New Zealand and *O. mordax* from Fiji. Gould's descriptions are inadequate for positive identification, but specimens which are in the Paris Museum from the type locality and which have been referred to by Lamy (1929) as *Ostrea forskali* Chemnitz var. *mordax* and var. *glomerata* are certainly not *commercialis*.

CRASSOSTREA ECHINATA (Quoy & Gaimard)

Plate 5, Fig. 4; Plate 6, Figs. 1-4

?Ostrea mytiloides Cox, 1883, p. 133; Hanley, 1856 (non Lamarck, 1819).
Ostrea echinata Quoy & Gaimard, 1835.
Ostrea spinosa Deshayes, 1836.
Ostrea mordax Cox, 1883, p. 130.
Ostrea nigromarginata Saville-Kent, 1891, p. 2, pl. 3, fig. 1; pl. 4, fig. 1; 1893, p. 245, chrom.-pl. 14, fig. 7; Hedley, 1909, p. 345 (non Sowerby, 1871).
Saxostrea gradiva Iredale, 1939, p. 400, pl. 7, fig. 10; Allan, 1950, p. 274.

Vernacular names: black-edge oyster or black-bordered oyster.

An adherent species, inequivalve; the largest Australian species of the genus and, like most species of *Crassostrea,* very variable in shape. The majority of specimens are elongate-oval in outline. The lower valve moderately deep, slightly folded, the lip with only a vague sinuation in specimens from sheltered waters, but exposed specimens have 8 or 9 regular crenulations, and in conjunction with these the lower valve is fluted. The upper valve rather flat, but usually with a definite central hump between hinge and lip. An upraised rim is characteristic of larger specimens and in exposed situations smaller specimens show it soon after leaving the spinous stage. Lamellar growth fringes show on shells from sheltered situations but they are lacking from oysters exposed to surf, presumably owing to the mechanical shock of the waves.

Young specimens of *C. echinata* are most distinctive amongst Australian oysters by having up to 24 spiny processes, jet black or deep purple in colour, set vertically from the shell surface of the upper valve. The hinge plate is moderately well developed and the hinge line rather short.

The external coloration is bluish or purplish black, often with a slaty grey patch near the hinge on the upper valve. In places exposed to sun and surf this slaty grey may cover the whole surface except for a black band inside the upraised rim. Internally the valves are white or greenish white with a broad deep purplish black band marginally, particularly well marked in the upper valve. The muscle scar is greenish white or white, though occasionally a jet black scar is found in the upper valve. The muscle scar is excavated on the hinge side. The upper valve bears a marginal row of denticles which are variably developed. In one of the largest specimens taken (15.4 by 10.4 by 5.5 cm) the denticles extended almost right around the rim, 37 ventrally and 25 dorsally, except on the most distal section of the lip; whereas others of equal size had only a few teeth on each side near the hinge, although traces of more anterior ones could be made out beneath the nacreous layer.

The gills are usually black-pigmented but sometimes they are cream with only a slight black suffusion; the palps are similar. The inner fold of the tentacle has moderately stout jet black tentacles which are fairly long, being 3-4 times their basal width in length; they are spaced 2-3 times their basal width apart except in the main inhalent region where there is only the basal width between adjacent tentacles. The inner row of tentacles on the mid fold are very long, being twice the length of the tentacles of the inner fold; they are white or cream in colour, with an occasional tentacle having a small patch of black pigment. The outer row of tentacles of the mid fold are translucent white, very short, and less than ½ the length of the tentacles of the inner fold. There are 4-8 of these outer row tentacles between each of the long inner row ones, though occasionally 2 adjacent inner row tentacles are found. The outer mantle fold is white; the groove between it and the mid fold is white or cream. The groove between the mid and the inner folds is black-pigmented, but the edge of the mid fold is cream, interrupted here and there by black. The inner fold is black-pigmented.

The anus opens just on the lip side of the adductor muscle and has a rich cream rim which contrasts with the usually black-pigmented epithelium of the rectum. Occasional specimens have the rectum cream also. The gills have 13-14 rods per plica. The auricles are narrowly joined.

Dimensions

Frequently growing to 7 by 5 by 2½ in.

Range

Along the Queensland coast from Gladstone to Thursday I. and along the Barrier Reef. An intertidal form in marine waters; attaches to rocks and mangrove roots. The range probably extends through the East Indies to the Moluccas.

Discussion

Ostrea echinata and *O. spinosa* were described from the same material collected by the *Astrolabe* at Amboina. Iredale suggested that these may be the young of *O. parasitica* Gmelin (= *O. mytiloides* Lamarck). Lamarck's type of *O. mytiloides* is not the species here identified as *Crassostrea echinata*. His type is not recessed under the hinge and has only a narrow purplish black margin internally and has a centrally placed muscle scar.

The occasional spinous young of other species (except *C. commercialis*) have the spines set at a low angle as continuations of the fold ridges. The very occasional spinous specimen of *C. commercialis* has pinkish grey, not black, vertical spines. Where *C. echinata* is common a series of intermediate stages with the spines becoming reduced in number can easily be located. Most 2-in. specimens have completely lost them. Hirase (1930) described a spinous young form under the name *O. echinata;* it is not, however, dark-spined but is pigmented like the Japanese species regarded by Hirase as being *O. cucullata,* and almost certainly is the young of that species.

O. nigromarginata Sowerby was described from Arakan. It has not been recorded from regions between there and northern Australia, so although Sowerby's description is inadequate, it seems hardly likely that the Australian species is identical. Specimens from Arakan in the Paris museum differ from this species in having a much wider hinge and having a wide dark internal border on the upper valve only. On the other hand some of the rim of the lower shell may be missing as the specimens are rather worn. They have only a few denticles lateral to the hinge. Nevertheless these are all rather variable characteristics; an examination of the anatomy of the soft body and comparison of the larvae is needed to determine whether 1 or 2 species are involved.

Iredale's *"Ostrea spinosa"* (1939) figured in his Plate 7, Figure 7, is a young *echinata.*

CRASSOSTREA AMASA (Iredale)

Plate 7, Figs. 1, 2

Ostrea mordax Saville-Kent, 1891, p. 2, pl. 12, figs. 1-4; 1893, pp. 65, 245, chrom.-pl. 14, figs. 1, 2 (non Gould 1850).

Ostrea forskali var. *mordax* Lamy, 1929, p. 164.

Saxostrea amasa Iredale, 1939, p. 399, pl. 17, fig. 8; Allan, 1950, p. 273, text fig. 65, fig. 1.

Vernacular name: coral rock oyster.

An adherent species, elongate, normally with a triangular cross section, the dorsal side of the shell being raised up, whereas the ventral edge is very low; however, occasional specimens which project beyond the rock substrate have the 2 sides almost of equal height, giving a quadrangular section. The lower valve is high-walled on the dorsal side, almost flat ventrally, deeply recessed under the hinge, with very distinct, even, moderately large crenulations around the rim rising from distinct flutings of the valve. The upper valve is very slightly domed and the lamellae are formed into rows of plicae radiating from the hinge; these are less distinct or eroded in exposed situations; the crenulated edge locks tightly into the lower valve. The hinge plate is long, the hinge width moderate. The external coloration is dull purplish pink. Internally the valves are chalky white with a narrow purplish black border between the crenulations; this extends right around on the upper valve, but is prominent only on the raised side of the lower valve. The muscle scar is markedly displaced distally and towards the lip. It may be white, purplish pink, or black. It is slightly raised on the lip side. A row of rather elongate denticles runs right around the edge of the upper valve.

The tentacles of the inner mantle fold are variably sized; they are rather broadly based and 3 times the basal width in length; they are spaced their basal width apart along most of the mantle but in the main incurrent and excurrent regions they lie close together. In life these tentacles are transparent with a bright yellow pigment spot near the tip and another larger one in the mantle fold at the base. The inner row of tentacles on the middle mantle fold are long and broad-based, about 3 times as long as the tentacles of the inner fold; they are rather variably spaced but generally are about 4 times their basal width apart. Each tentacle has a large yellow pigment patch at the base, and towards the upper ⅓ another which on some tentacles is partially obscured by a suffusion of brown or black pigment. Towards the hinge the tentacles are smaller and the pigment spots less intense in colour. The outer row of tentacles on the middle fold are fairly uniform in size, about 3 times their basal width in length, but smaller than the tentacles of the inner fold. They are translucent white, variably suffused with yellow and black pigments. The outer fold is unusual in being black, though towards the hinge on the upper mantle the pigment is not so intense as elsewhere. The outer groove of the mantle is very distinct; the groove between the mid and inner folds is clear white on the inner fold side, but is black-pigmented with yellow splotches on the mid-fold side. The inner surface of the inner fold is pigmented a brown colour with patches of black, with a darker brown band running circularly just below the yellow spots at the base of the tentacles. No grooving of the mantle is apparent in the excurrent or incurrent regions. The gills have 12 rods per plica. They are grey or cream with dark pigment spots at the free ends.

Range

From Bundaberg northwards along both the Barrier Reef and mainland shores to the Torres Strait Is. and to the Gulf of Carpentaria; probably into the Northern Territory. A marine oyster of the intertidal zone, closely adherent to rocks.

Discussion

This species might be the same as *Ostrea lingua* Lamarck from Timor. But the type specimens of *lingua* are much weathered, apparently being beach-collected material. As a result it is impossible to distinguish the original characteristics of the shells. The species recognized here as *Crassostrea amasa* agrees with Lamy's (1929) *Ostrea forskali* var. *mordax* from New Caledonia; but whether it is *mordax* Gould is uncertain owing to the inadequacy of the original description.

CRASSOSTREA SEDEA (Iredale)

Plate 7, Figs. 3, 4; Plate 8, Figs. 1, 2

Ostrea sedea Iredale, 1939, p. 397, pl. 17, fig. 5.

Adherent usually only near the hinge end, fairly uniformly elongate-oval in shape, characterized by the abruptly upturned rim of the lower valve, slightly recessed under hinge; upper valve rather concave on outer surface, almost all the internal cavity being formed in the lower valve. The upper valve shows strong fluting; the lips are rounded, there being no crenulations. The hinge line is very short, and the hinge plate narrow. The ligament is light brown. External coloration dull cream to dirty yellow, frequently with purple rays. Internal coloration chalky white or greenish with purple colour showing through and a light brown or purple border. The muscle scar is white or rarely greenish and is flattened on the hinge side. Denticles absent.

The inner fold of the mantle bears small tentacles which are white laterally or sparsely pigmented with brown near the tip; about twice as long as the basal width and 4 times the basal width apart; the mid fold bears 2 rows of brown-pigmented tentacles of which the inner are relatively long, about 7 times the basal width and spaced with 3-4 outer row tentacles between; the outer row of tentacles shorter, only twice the basal width. The inner mantle fold is lightly suffused with brown, the middle fold similar but with more intense pigmentation at the base of the long tentacles; laterally these basal spots are the only pigmented portion of the fold. The gills and palps are creamy yellow; only 7 bars per plica. No grooving of the mantle is apparent in the exhalent and inhalent areas. The auricles are only narrowly joined. The rectum is free, not attached along its whole length to the adductor muscle. The anus opens some distance short of the lip end of the adductor.

Dimensions

The largest specimen seen was 1¼ in. long. Specimens less than an inch long seem to be mature.

Range

Iredale recorded the species only from Lindeman I., Michaelmas Cay, and Low Is., all on the Barrier Reef. It is also common on submerged surfaces around the Torres Straits Is., along the west coast of the York Peninsula (specimens from Batavia R.) and Groote Eylandt. Dredgings in Moreton Bay, southern Queensland, have shown it to be common there also. Usually taken on submerged objects, but considerable numbers have been taken intertidally at Amity Banks, Moreton Bay, and at the mouth of the Batavia R.

Discussion

This species has probably been overlooked as a probable juvenile of another species by most collectors. It simulates closely the young of *Crassostrea commercialis* and has been mistaken for such by commercial oystermen on the Amity Banks in Moreton Bay.

CRASSOSTREA TUBERCULATA Lamarck

Plate 8, Fig. 3

Ostrea tuberculata Lamarck, 1819, p. 202; Lamy, 1929, p. 76.

Ostrea cucullata Lamarck, 1819, p. 200; Hornell, 1917, p. 15, fig. 3; Awati and Rai, 1931; Hirase, 1930, p. 25, fig. 39 (non Born, 1780).

Vernacular name: north-west rock oyster.

A recumbent species, the lower valve being closely adherent; with a large recess under the hinge, distinctly fluted, the folds being definite and sharply ridged, ending in a distinctly crenulated lip. The upper valve opercular, flat dorso-ventrally but arched from hinge to lip; surface without definite sculpture except for the marginal crenulations which fit the lower valve almost horizontally; the hinge line wide, the hinge plate often very prolonged; the ligament brown. Externally the shell is pinkish purple, often bleached almost white; the muscle scars are displaced away from the hinge, being less than their own width from the lip. The scar is variably white flecked with purplish black or entirely the latter colour. The scar in the lower valve is flattened or even excavate on the side nearest the hinge; scar in the upper valve is often rather rounded or even pointed on the hinge side. Numerous denticles.

The mantle, gill bars, and extremities of the gills are pigmented in black. The tentacles of the inner fold are 2½-3 times their basal width in length, and black-pigmented; the inner row of the mid fold long, about 6 times the basal width, heavily pigmented with black, with about 4-7 outer row tentacles between each pair of inner ones; outer row tentacles short, about 2½ times basal width in length and the basal width apart, suffused with black. The edges of the mid and inner folds black-pigmented, becoming less intense laterally and anteriorly.

Range

Extends from the Abrolhos Is. and along the main Western Australian coastline from the mouth of the Murchison R. northwards. The northern limit is unknown but the species extends at least to the vicinity of Broome. It is taken as a subfossil in the Swan R. and at Albany further south along the Western Australian coast.

Discussion

The north-western Australian specimens agree very well with the oysters known as *Ostrea cucullata* in India. Hirase's (1930) description and photo are not precise enough to make certain of the identity, but the

Japanese species is very similar. Despite the widespread use of this name for cucullated species in the Indo-Pacific, it is doubtful, according to Roughley (1928) and Iredale and Roughley (1933), whether this name is correctly applied, as Born's specimens came from Ascension I. in the Atlantic. The descriptions of *O. cucullata* by Born (1780), Lamarck (1819), and by Hanley (1856) do not distinguish the species from several other cucullated types. The name *cucullata* has been applied to one Japanese species by Lischke (1871), Dunker (1882), and Hirase (1930); Morse (1879), Mitsukuri (1906), and Iwakawa (1919) have used it for another (actually *Crassostrea gigas*); Krauss (1848) has used the name for a South African oyster; Macandrew (1870) applied it to an oyster from the Gulf of Suez; Hedley (1909), Roughley (1926), and Boone (1938) have all called the Australian commercial oyster (*Crassostrea commercialis*) by this name.

Crassostrea scyphophylla (Peron) may be an ecomorphic form of this species, although Iredale (1949) has recently regarded it as valid. The peculiar chambering of the tube-like lower valve may be simply a result of the animal's desperate attempts to keep its rim above that of its fellows, and, being unable to prolong its body and organs indefinitely, it has resorted to chambering. If it is the same species then name *scyphophylla* takes precedence.

CRASSOSTREA GIGAS (Thunberg)

Plate 8, Fig. 4; Plate 9, Figs. 1-4; Plate 10, Fig. 1

Ostrea gigas Thunberg, 1793, p. 140, figs. 1-3; Lischke, 1871, p. 174; Dunker, 1882, p. 249; Pilsbry, 1895, p. 145; Iwakawa, 1919, p. 254; Takatsuki, 1927, p. 22; Amemiya, 1928, p. 334; Hirase, 1930, p. 45, figs. 61-64; Gunter, 1950, p. 446 (non Humphrey, 1797).

Ostrea laperousi Schrenk, 1867, p. 475, pl. 19, figs. 1-6; Wakiya, 1929, p. 359, pl. 8, figs. 1-3; Hirase, 1930, p. 49, figs. 65-80.

Ostrea talienwhanensis Crosse, 1862, p. 149, pl. 6.

Ostrea cucullata Morse, 1879; Mitsukuri, 1906, p. 524; Iwakawa, 1919, p. 254.

Vernacular names: Pacific oyster; Japanese oyster.

An adherent species, markedly inequivalve, very variable in shape. The lower valve deep, cup-shaped, recessed under the hinge, rather strongly but unevenly folded externally, with strong but wide and uneven crenulations along the lip; the upper valve is rarely flat, usually humped or domed, though its concavity is slight compared with that of the lower valve; it is strongly crenulate to form a tight fit with the lower valve. The hinge plate is moderate and the hinge line moderately wide. The external colour is variably white or creamy yellow in ground colour with purple or sometimes reddish streaks radially from the hinge, usually interrupted in older specimens. Internally the shells are faintly opalescent white with a dull purple or light brown border; the muscle scars are white or pale yellow with occasional purple patches, particularly in the upper valve. The ligament is purple or yellowish brown in colour. There are no denticles.

Laterally the tentacles of the inner fold are twice their basal width in length and are their own basal width apart; near the lip, where they are elongate, they are swollen 7 times their basal width in length. The middle tentacles laterally are similar to other species, having well-spaced long inner row tentacles with 5-6 small outer row tentacles between them. The marginal tentacles right round are 1$\frac{1}{2}$-2 times their basal width apart. The inner row tentacles are 5 times their basal width along the lateral margins, but in the incurrent and excurrent areas they are swollen and are 7-9 times the basal width and are very close together so that they overlap. All the tentacles are fairly evenly pigmented with light brown. The inner face of the inner fold is similarly pigmented and below it is an area of black pigment. The outer groove is rather deep and is unusual in having the inner face pigmented, though only lightly.

The pallio-branchial fusion is on the dorsal side but remote from the adductor on the lip side. The heart auricles are very narrowly joined and coloured light brown. The rectum does not reach more than $\frac{2}{3}$ of the distance along the adductor. There are 12-14 gill bars to a plica.

Range

This oyster is a native of the Japanese main islands, Hokkaido, Honshu, and Kyushu. It has been imported into Australia (Thomson 1952); at present it is restricted to Pittwater, Tas.

Discussion

Wakiya (1929) preferred the name *laperousi* Schrenk on the grounds that *O. gigas* Thunberg was a homonym of *gigas* Meuschen (1787). But Meuschen's *gigas* was not an ostreid, but a species of *Chama*. *Ostrea gigas* Humphrey (1797) was a new name for the ponderous *Pycnodonte hyotis* (Linnaeus). Hirase (1930) also preferred *laperousi* on the grounds that the true *gigas* is the large oyster found along the northern coast of Hokkaido. But most authors regard this as merely a cold-water form of one species of which *laperousi* is the warm-water representative. Complete intergrades exist and Professor Imai of Tohoku University (personal communication) finds the 2 forms to interbreed freely under controlled conditions. This is certainly not the same species as the Indian *cucullata*. Wakiya (1929) discussed this misnomer.

3. Genus PYCNODONTE Fischer de Waldheim

PYCNODONTE HYOTIS (Linnaeus)

Plate 10, Figs. 2-4; Plate 11, Figs. 1-3.

Mytilus hyotis Linnaeus, 1758, p. 704; Dillwyn, 1817, p. 300; Wood, 1828, p. 12, fig. 1.

Ostrea gigas Humphrey, 1787, p. 53.

Ostrea hyotis Chemnitz, 1780, fig. 683; Lamarck, 1819, p. 203; Deshayes, 1836, p. 298; Hanley, 1856; Sowerby, 1871, pl. 4; Lamy, 1929, p. 232.
?Ostrea radiata Lamarck, 1819.
Ostrea cristagalli Saville-Kent, 1891, p. 1, pl. 13, fig. 2; 1893, p. 244, chrom.-pl. 14, fig. 5 (non Linnaeus, 1758).
Ostrea cerata Hedley, 1906 (non Sowerby, 1871).
Lopha hyotis Iredale, 1936, p. 269; 1939, p. 401; Allan, 1950, p. 275, pl. 29, fig. 3.
Ostrea procles Iredale, 1939, p. 396, pl. 17, fig. 2; Allan, 1950, p. 275.
Pycnodonta hyotis Ranson, 1941.

Vernacular names: hyotid oyster, giant oyster.

Adherent basally, this oyster grows to a large size with ponderous shells; lower valve massive, slightly recessed under hinge, without definite sculpture except near the lip where obsolescent flutings are apparent, terminating in sharp crenulations along the lip. The upper valve is similar except that there is no recess; in large specimens the surfaces of both valves are largely eroded by the action of boring sponges and other organisms. In younger specimens the folds on the surface are more apparent and may be produced into tubular spines. The hinge is very broad and the hinge plate long. Externally the shells show traces of brown or purplish pigmentation on a yellowish ground, but generally they are white where the encrusting plants and animals have covered the shell. Young specimens are uniformly brown or purplish. Internally the shells are chalky white, or greenish with a broad brown border; the muscle scar is usually white with radiating brown streaks in the lower valve and greenish on the upper; the muscle scar is peculiarly elevated to form a shelf-like projection with the higher side away from the hinge; its shape is elongate-oval, the hinge side of the muscle and scar being rounded. On both valves there are subtubular denticles which are prolonged at right angles to the valve edge. Adjacent to the hinge on each side are triangular patches of small closely set ridges, probably representing the tubular denticles of an earlier growth stage. One or 2 similar patches are visible below the hinge plate, ½ covered by shell material. Although the lower valve is more massive, the cavities of the 2 valves are subequal.

The inner fold of the mantle has a row of closely set short lobate tentacles, about as long as wide and white in colour. The middle fold bears 2 rows of stout club-shaped tentacles, the inner row being slightly longer, but reaching only as far as the outer row so that a uniform edge is presented. The outer fold is without tentacles and it and the groove between it and the middle fold are a translucent white. A fringe of rust-brown pigment on the inner side of the middle fold extends as a light suffusion on to the inner side of the tentacles, more so on the upper mantle than on the lower; the groove between the middle and inner folds is very broad, at the bottom of which is a silvery pigment-free band; a broad rust-brown border runs on to the inner fold.

The mantle is deeply grooved in the exhalent region but only slightly elsewhere; the ridges of the mantle in this exhalent area are pigmented with brown. The rectum runs unusually far posteriorly, projecting markedly beyond the adductor muscle almost to the mantle junction. The anus is not circular in outline but compressed with a ventral groove and peculiar fold in the right ventral corner. The adductor muscle is an elongate-oval in outline and is rounded on the hinge side, in contrast with *Ostrea* and *Crassostrea*, where the hinge side of the adductor is either straight or incurved.

The gills and palps are off-white or cream in colour. The gonad instead of being the white or cream usual to ostreids is bright orange. The auricles of the heart are broadly joined. The ventricle is penetrated by the rectum, but not for its entire length, there being a free portion of the ventricle lying in the pericardium before surrounding the rectum.

The young of *Pycnodonte hyotis* are sufficiently dissimilar from the ponderous adult shells to have received a separate name, *Ostrea procles* Iredale. The following details differ from the adult appearance. The shell is often closely adherent, flattened, suborbicular; the lower valve is very shallow, displaying indefinite flutings which are more apparent in only partially adherent specimens; the rim is gently waved in regular but weak crenulations which gradually become more pronounced with size. The upper valve is domed and not infrequently has a bigger cavity than the lower valve. There is a marked upraised internal rim within which the bulk of the oysters lie. The hinge line is broad but the hinge plate narrow, the ligament being dark purple or black. Externally the valves are pale pellow with indistinct reddish purple lines, which are distinct only near the lips and radiate from the hinge. Internally the valves are chalky white or greenish and towards the edge beyond the upraised rim, the honeycomb - chambering described by Ranson (1941) is clearly apparent (Fig. 44). This is covered by the nacreous layer as the shell grows but is always somewhat visible laterally and can be found by sectioning the shell.

The external folds and swellings adjacent to the hinge are obvious at an early stage, clearly linking the young to the adult type. The shell of the young is very chalky, being easily cut into by the thumbnail. Internally the same rust-brown pigment as is found in the adult suffuses the mantle and the mid-fold tentacles. The pigmented border of the inner fold is interrupted by patches of white in the young forms. Denticles are lacking in the smaller specimens.

Dimensions

Massive when old, the largest measured by the author being 19 cm long, 14.5 cm wide, and 12 cm deep, the lower valve alone being 10.6 cm deep; the lower valve cleaned of encrusting organisms weighed 3 lb and the upper valve 1 lb 5 oz . Saville-Kent (1893) recorded specimens up to 7 lb and 30 cm in length.

Range

Along Australian coasts from the Great Barrier Reef along the north of Australia to North-west Cape, W.A. It is taken as a subfossil in dredgings near Sydney (Iredale 1936). Usually submerged, some specimens being attached high enough to come out of water at low spring tides. They are often attached to coral masses and occur on the wharf piles at Thursday I.; a specimen from North-west Cape was attached to a gorgonid.

Discussion

This is the *hyotis* and *procles* of Iredale (1939) and Allan (1950), but it does not appear to be the *Ostrea* (*Lopha*) *hyotis* of Hirase (1930), where neither description nor photograph show the typical tubular denticles which Lamarck (1819), Hanley (1856), and Ranson (1941) described. Deshayes (1836) and Hanley (1856) stated that *O. radiata* Lamarck was probably founded on an aged specimen of *Hyotis*. Deshayes also considered that *O. imbricata* Lamarck recorded from Java was also a form of *hyotis*. But Dunker (1882) and Hirase (1930) identified another oyster from Japan as *imbricata,* and, apart from the fact that some young *hyotis* tend to send out tubular spines from the ribs as in *imbricata,* there does not seem much in common in the original descriptions. The large cock-comb oyster of Saville-Kent is undoubtedly this species, not *crista-galli* (= *folium*) Linnaeus as he records it. Although at first sight the young of this species looks unlike the old shellfish its conchological and malacological characters leave no doubt as to their being *hyotis*. The peculiar ridges laterally to the hinges, the honeycomb chambering, and the ventricle passing on to the rectum all point conclusively to the identity of large and small species.

KEY TO AUSTRALIAN SPECIES OF THE FAMILY OSTREIDAE

Two keys will be given, one based on shell characters, and one based on the malacological characters.

A. Key Based on the Shell Characters

1. Recessed under hinge, muscle scar displaced dorsally, denticles when present on upper valve only; live shell firm (Genus *Crassostrea*) 2
   Not recessed under hinge; muscle scar central; denticles when present on upper valve only; live shell firm (Genus *Ostrea*) 7
   Not recessed under hinge or only very slightly; muscle scar displaced dorsally; vermicular denticles on both valves; live shell chalky and having a microscopic honeycomb structure .. .. *Pycnodonte hyotis*

2(1). Denticles absent 3
   Denticles present 4

3(2). Small species; upper valve flat; internal colour chalky white or greenish with purple marks .. .. *C. sedea*
   Large species; upper valve domed; internal colour faintly opalescent white with occasional purplish patches .. .. *C. gigas*

4(2). Shell cavity elongate-oval in cross section; upper valve broadly laminate or smooth 5
Shell cavity triangular in cross section; upper valve with rows of plicae .. .. *C. amasa*

5(4). Valves with only moderate internal pigmented margins 6
Valves with broad purplish black margins internally .. .. *C. echinata*

6(5). Ligament blue-black; hinge moderate; denticles prominent only near hinge .. *C. commercialis*
Ligament brown; hinge wide; numerous prominent denticles from hinge to the lateral corners .. .. *C. tuberculata*

7(1). Outline not circular; prismatic layer reduced and not in broad scales; opalescent internally 8
Outline circular; concentric broad laminate prismatic scales; dull white internally .. .. *O. angasi*

8(7). Crenulations indefinite or broadly obtuse; external colour greenish white with purple or red pigmentation in streaks (if present) 9
Crenulations sharp; external colour bright bronze (or rarely purple) uniformly suffused .. .. *O. folium*

9(8). External pigmentation includes streaks of red or purple; internally a border of contrasting .. .. *O. trapezina*
External pigmentation without red or purple streaks; no contrasting border internally .. .. *O. nomades*

B. Key Based on the Soft Anatomy

1. Ventricle not surrounding the rectum 2
Ventricle surrounding the rectum .. .. *Pycnodonte hyotis*

2(1). Without a promyal chamber (Genus *Ostrea*) 3
With a promyal chamber (Genus *Crassostrea*) 6

3(2). Gills and palps greenish grey or white 4
Gills and palps bronze-red .. .. *O. folium*

4(3). Length of tentacles of inner mantle fold twice basal width or less; light brown suffusion or no pigmentation on mantle edge 5
Length of tentacles of inner mantle fold 3-4 times basal width; heavy brown suffusion on mantle edge .. .. *O. angasi*

5(4). Tentacles of inner mantle fold $\frac{1}{4}$-$\frac{1}{2}$ basal width apart; outer row of tentacles of the mid fold spaced 2-4 between each of inner row tentacles .. *O. trapezina*
Tentacles of inner mantle fold 2-3 times basal width apart; outer row of tentacles of the mid fold spaced 5-6 between each of inner row tentacles .. *O. nomades*

6(2). Pigment spots at base of inner fold tentacles and of mid fold tentacles black or brown 7
Pigment spots at base of inner fold tentacles and of mid fold tentacles yellow *C. amasa*

7(6). Gills and palps cream 8
Gills and palps brown or black 9

8(7). Gill filaments 7 per plica .. .. *C. sedea*
Gill filaments 13-14 per plica .. .. *C. commercialis*

9(7). Pigmentation on mantle and tentacles black; inner row of tentacles on the mid fold not overlapping 10
Pigmentation on mantle and tentacles brown; inner row of tentacles of mid fold clearly overlapping .. .. *C. gigas*

10(9). Outer mantle fold white; outer row of tentacles of mid fold translucent white *C. echinata*

Outer mantle fold black; outer row of tentacles of mid fold suffused with black *C. tuberculata*

V. ACKNOWLEDGMENTS

M. Gilbert Ranson, malacologist of the Muséum Nationale d'Histoire Naturelle de Paris, readily gave access to the types of Lamarck and to the collection of Ostreidae in the museum. The author acknowledges his indebtedness to his colleagues, Mr. J. S. Hynd, Mr. A. M. Olsen, Mr. F. Allen, and to the field staff of the C.S.I.R.O. Fisheries laboratory at Thursday I. Mr. R. Breach, under the direction of Mr. A. Proctor, prepared the excellent photographs.

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EXPLANATION OF PLATES 1-11

PLATE 1

Fig. 1.—*Ostrea angasi*, upper valve.
Fig. 2.—*O. angasi*, lip view.
Fig. 3.—*O. angasi*, internal view of shell.
Fig. 4.—*O. trapezina*, external, lower valve (left) and upper (right).

PLATE 2

Fig. 1.—*Ostrea trapezina*, lip view.
Fig. 2.—*O. trapezina*, internal view.
Fig. 3.—*O. folium* (*bresia* type). Note white streak from umbo.
Fig. 4.—*O. folium* (*folium* type).

PLATE 3

Fig. 1.—*Ostrea folium* (*crista-galli* type), lip view.
Fig. 2.—*O. folium* (*bresia* type), lip view.
Fig. 3.—*O. folium* (type intermediate between *crista-galli* and *bresia*), lip view.
Fig. 4.—*O. folium*, internal view.

PLATE 4

Fig. 1.—*Ostrea nomades*, upper valve.
Fig. 2.—*O. nomades*, lip view.
Fig. 3.—*O. nomades*, internal view, white patches show where shell broke on lifting from substrate.
Fig. 4.—*Crassostrea commercialis*, upper valve.

PLATE 5

Fig. 1.—*Crassostrea commercialis*, lower valve.
Fig. 2.—*C. commercialis*, lip view.
Fig. 3.—*C. commercialis*, internal view.
Fig. 4.—*C. echinata*, upper valve.

PLATE 6

Fig. 1.—*Crassostrea echinata*, lip view.
Fig. 2.—*C. echinata*, internal view.
Fig. 3.—*C. echinata*, upper valve (young spinous form).
Fig. 4.—*C. echinata*, upper valve lateral (young spinous form).

Plate 7

Fig. 1.—*Crassostrea amasa*, dorsal valve, showing lateral gape.
Fig. 2.—*C. amasa*, internal view upper valve.
Fig. 3.—*C. sedea*, upper valve.
Fig. 4.—*C. sedea*, lateral view.

Plate 8

Fig. 1.—*Crassostrea sedea*, lip view.
Fig. 2.—*C. sedea*, internal view.
Fig. 3.—*C. tuberculata*, dorsal view showing internal view of one shell.
Fig. 4.—*C. gigas* grown on shifting sand (upper valve).

Plate 9

Fig. 1.—*Crassostrea gigas* grown on shifting sand (lower valve).
Fig. 2.—*C. gigas* grown on wire tray (upper valve).
Fig. 3.—*C. gigas* grown on wire tray (lower valve).
Fig. 4.—*C. gigas*, lip view.

Plate 10

Fig. 1.—*Crassostrea gigas*, internal view.
Fig. 2.—*Pycnodonte hyotis*, upper valve.
Fig. 3.—*P. hyotis* (*procles* type), external view.
Fig. 4.—*P. hyotis* (*procles* type), internal view.

Plate 11

Fig. 1.—*Pycnodonte hyotis* (adult), internal view.
Fig. 2.—*P. hyotis*, lip view.
Fig. 3.—Photomicrograph of honeycomb area in young specimen of *P. hyotis*.

List of Species

Genus *Crassostrea*

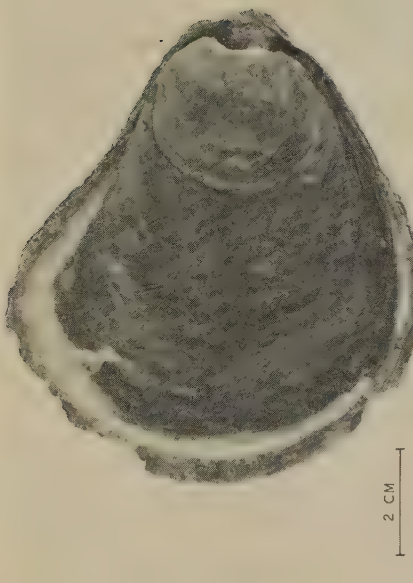
C. amasa (Iredale) 154
C. commercialis (Iredale & Roughley) 150
C. echinata (Quoy & Gaimard) .. 151
C. gigas (Thunberg) 158
C. sedea (Iredale) 156
C. tuberculata Lamarck 157

Genus *Pycnodonte*

P. hyotis (Linnaeus) 159

Genus *Ostrea*

O. angasi Sowerby 143
O. folium Linnaeus 146
O. nomades Iredale 149
O. trapezina Lamarck 145



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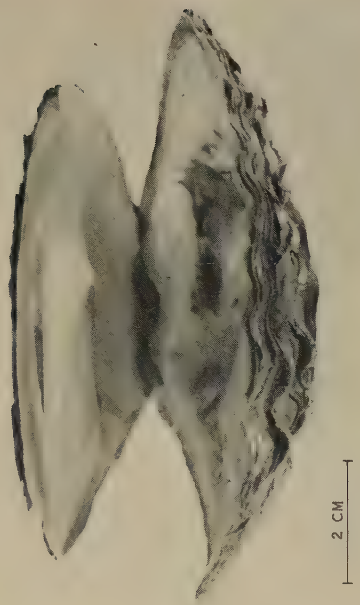

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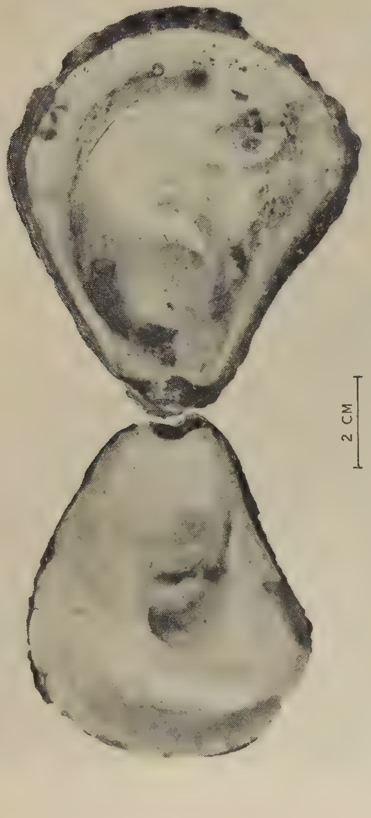

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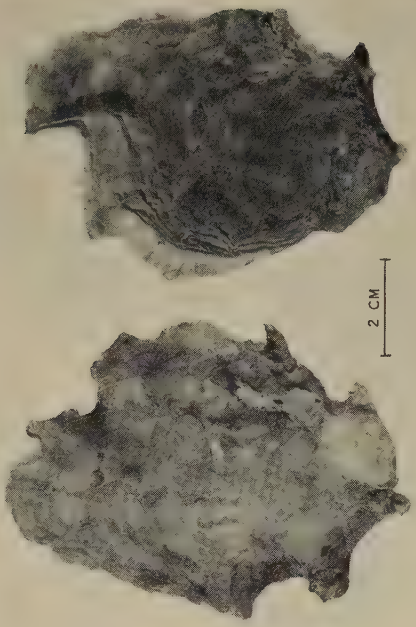

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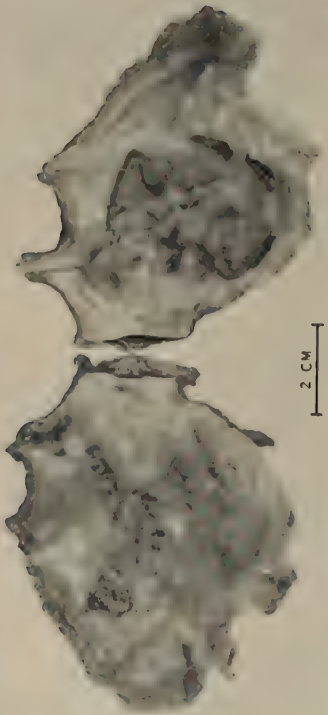

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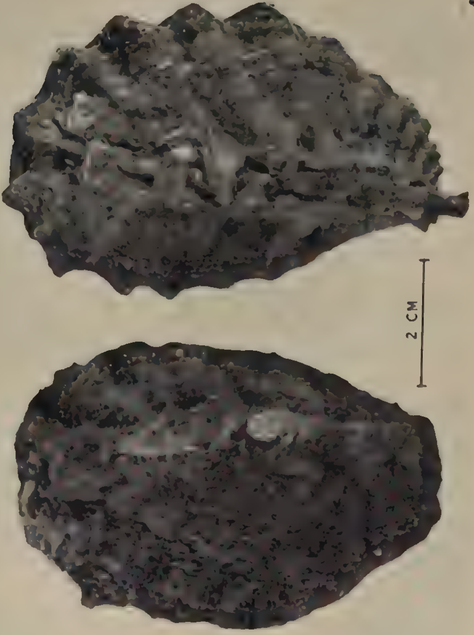

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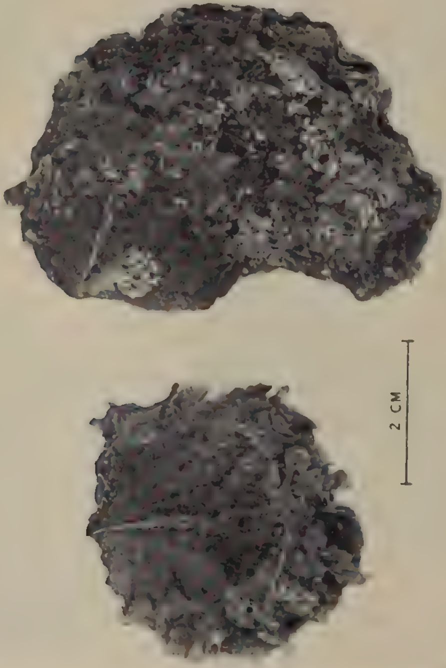

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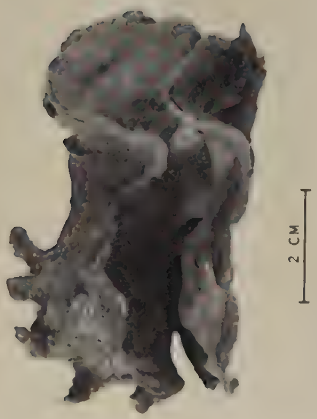

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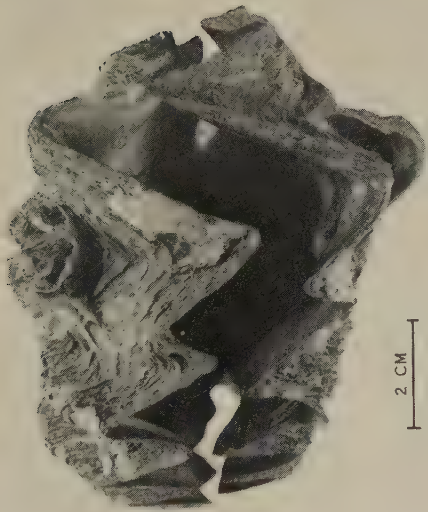

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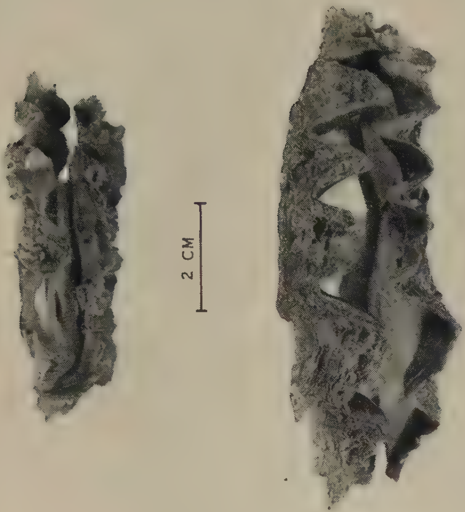

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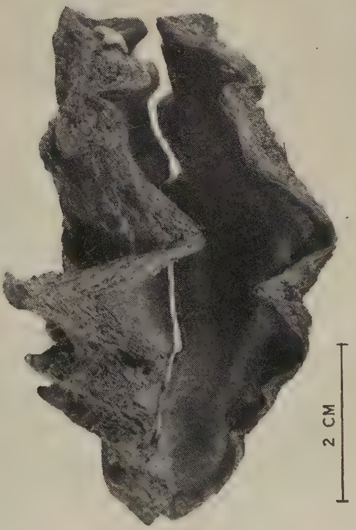

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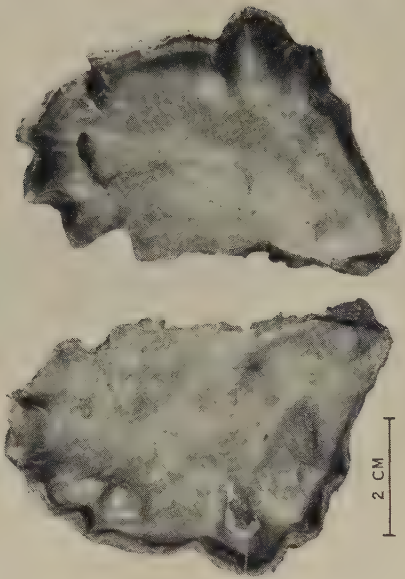

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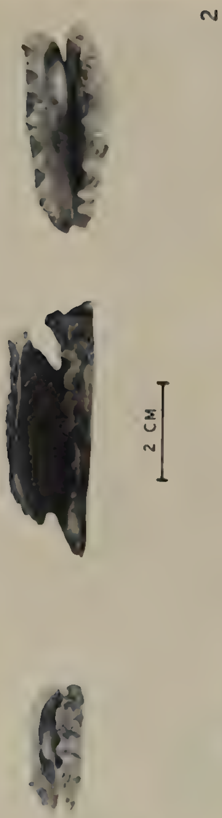

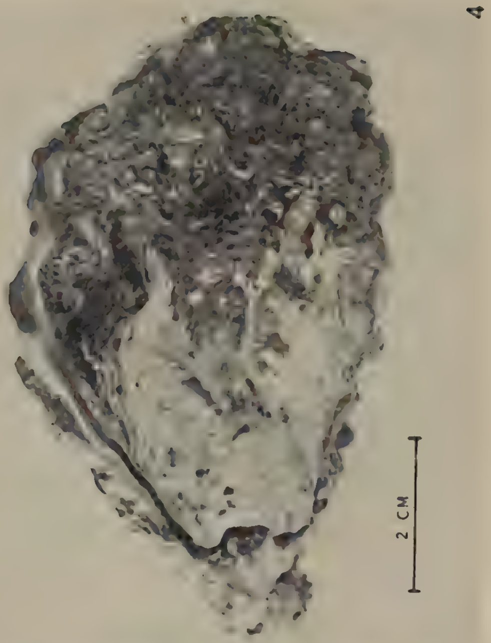

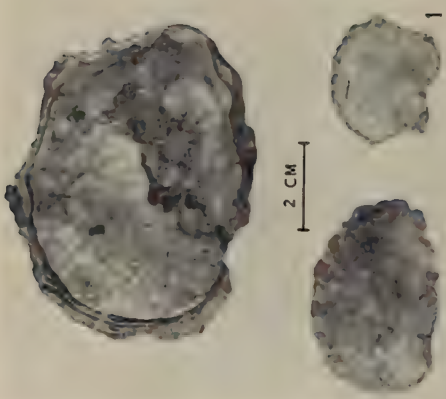

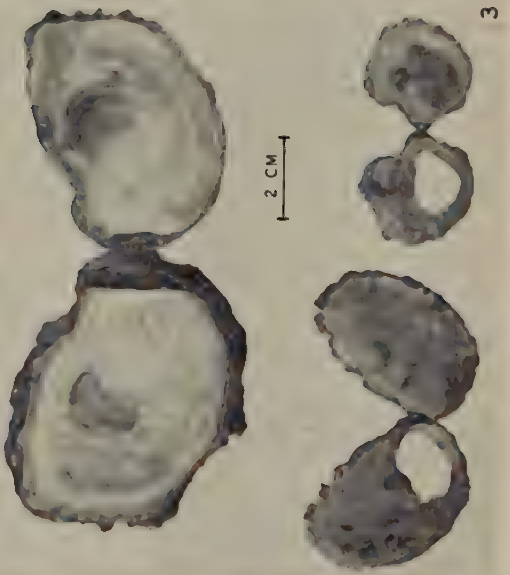

PLATE 5

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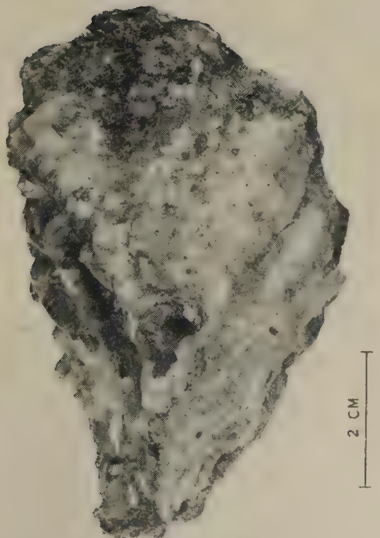

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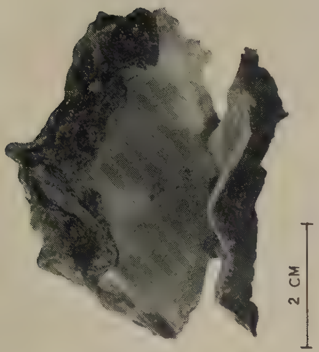

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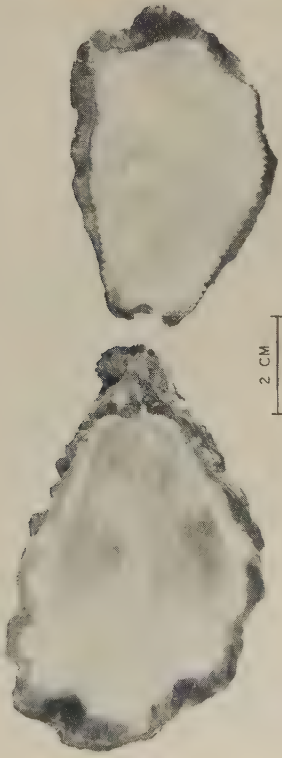

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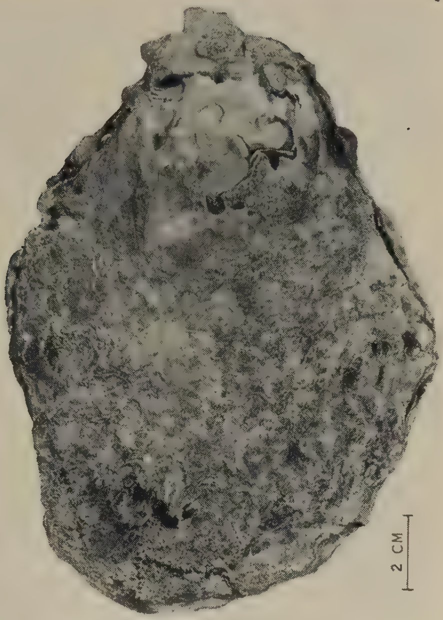

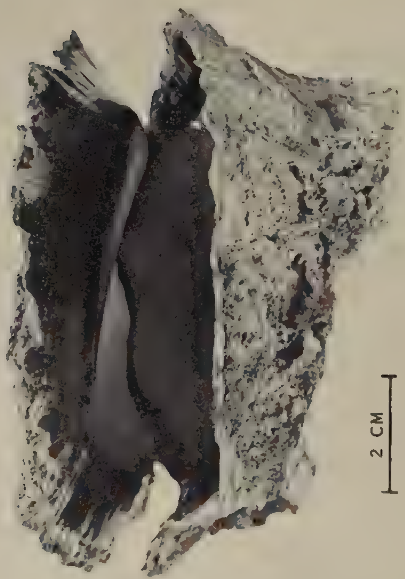

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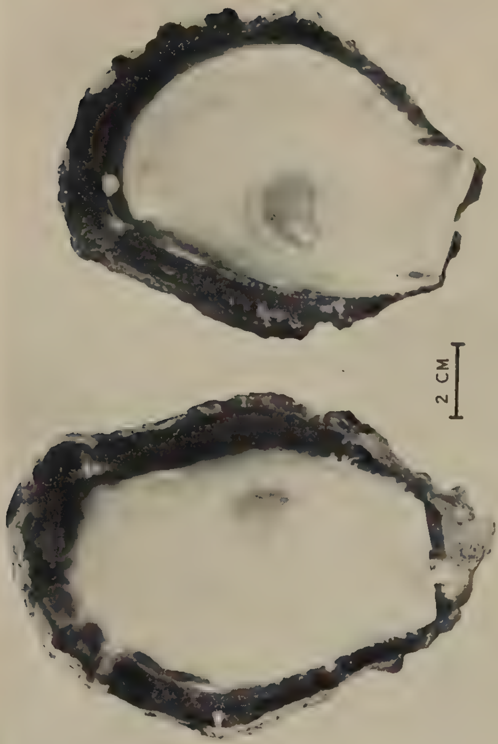

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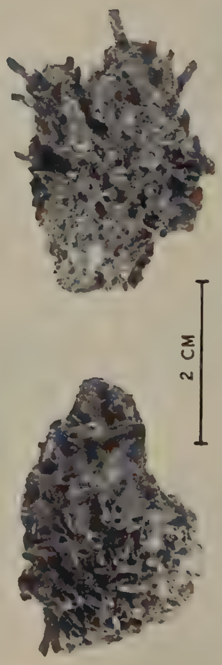

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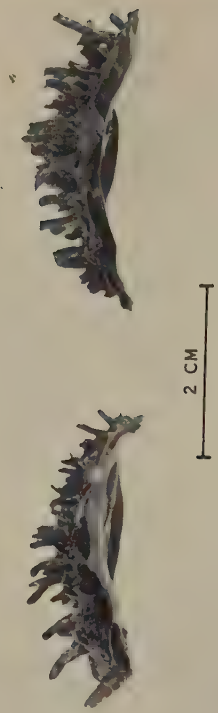

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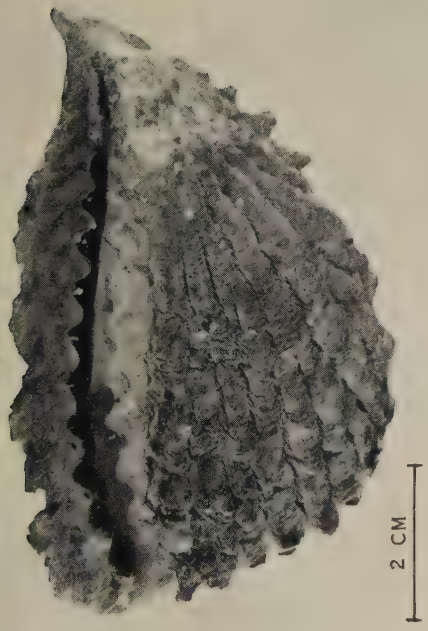

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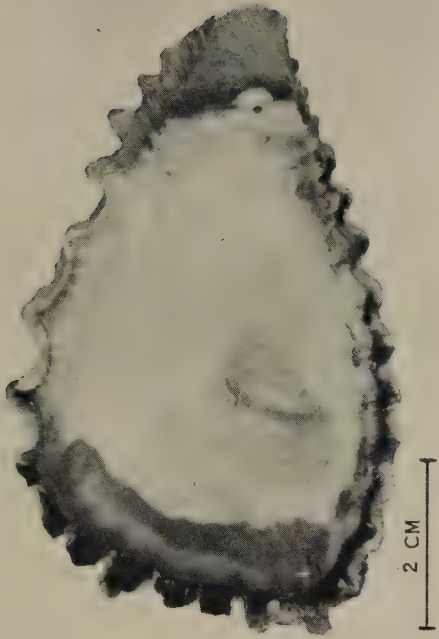

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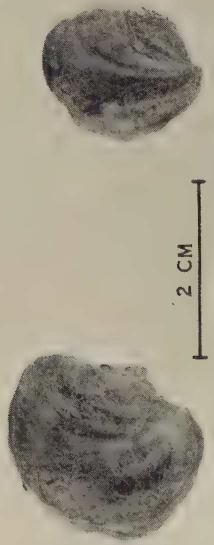

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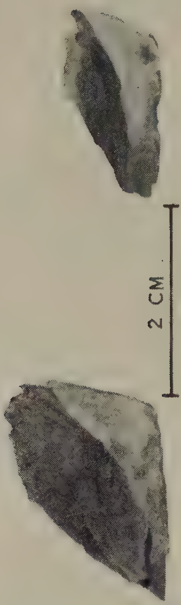

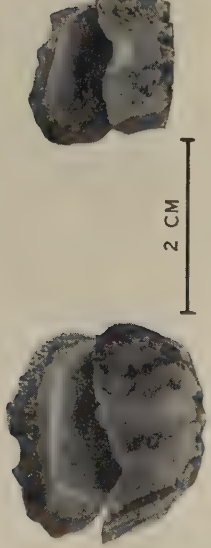

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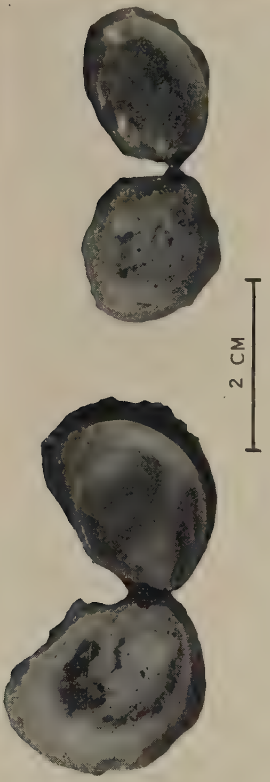

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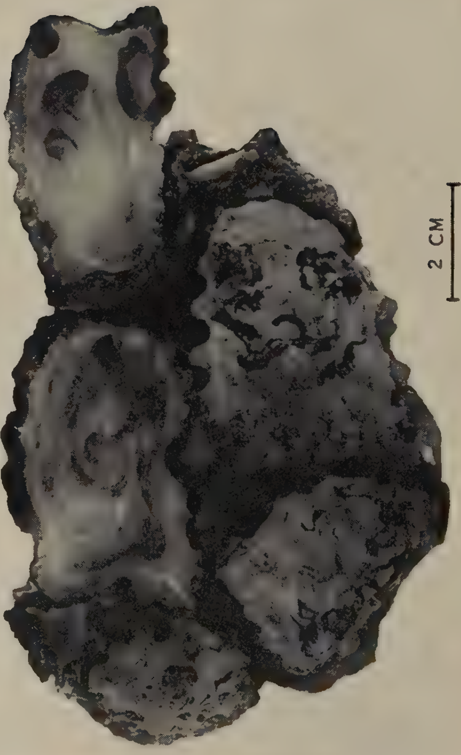

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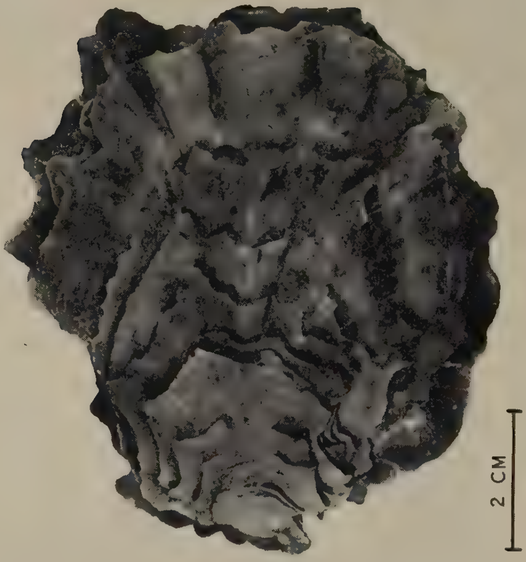

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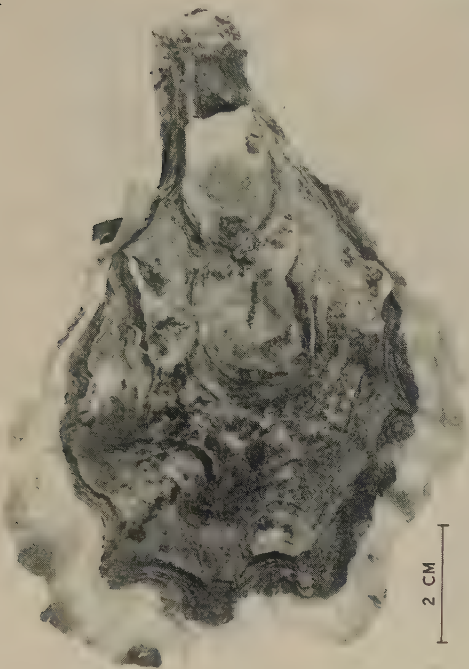

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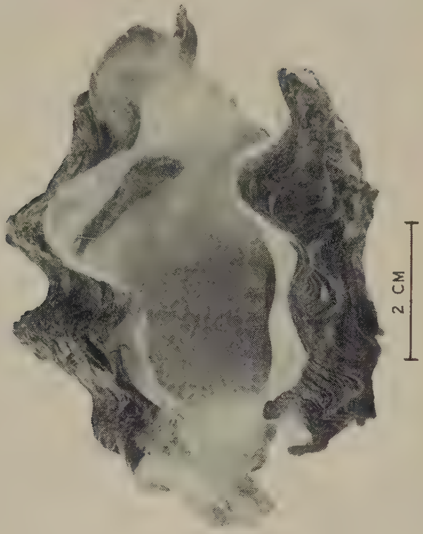

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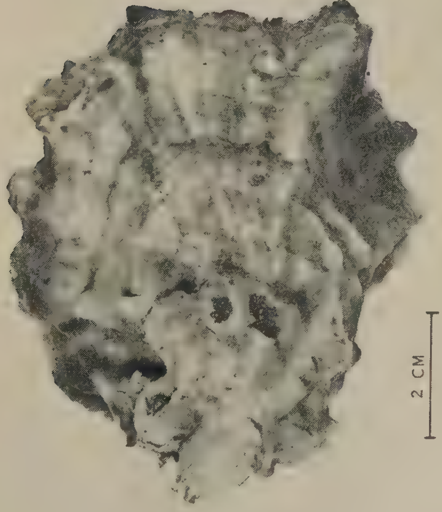

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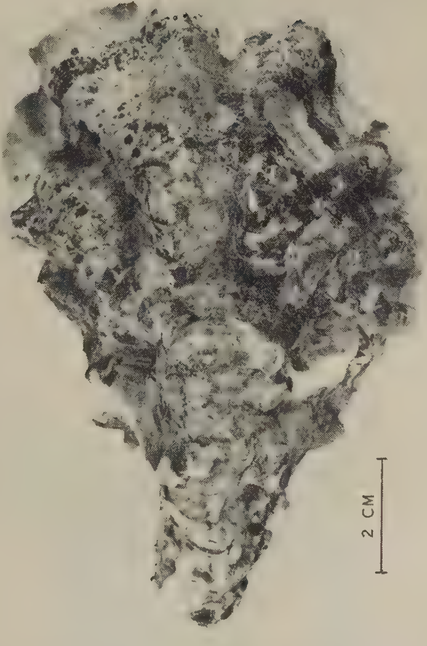

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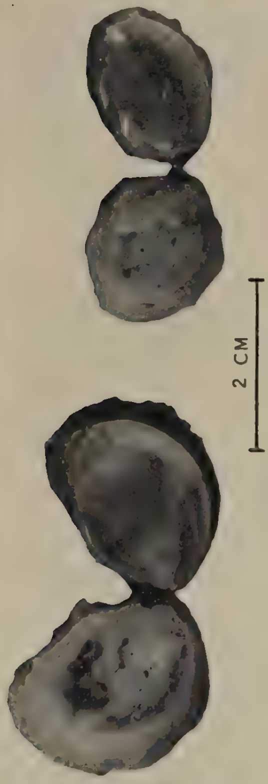

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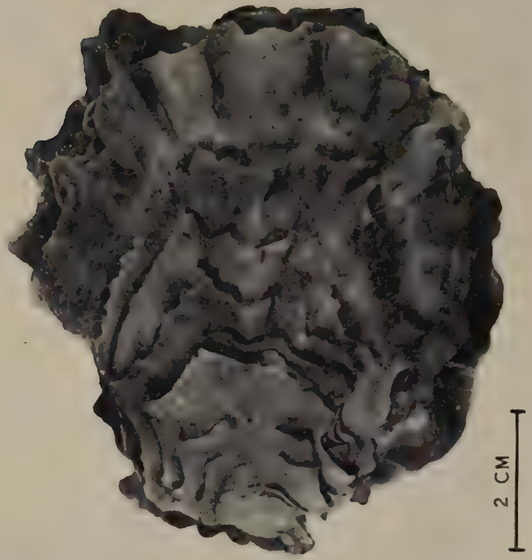

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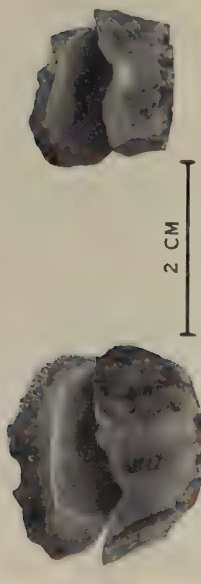

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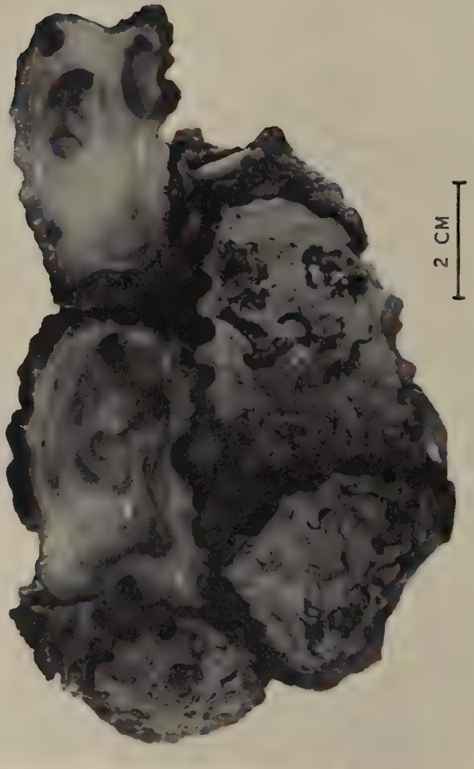

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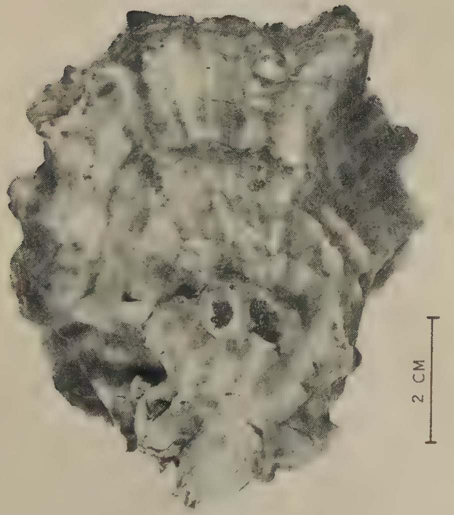
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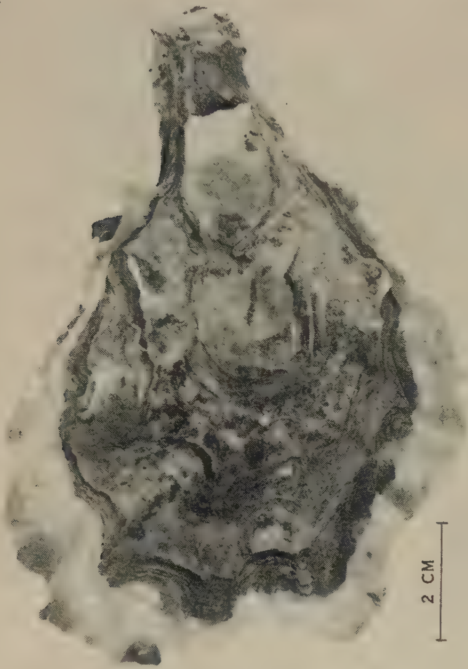
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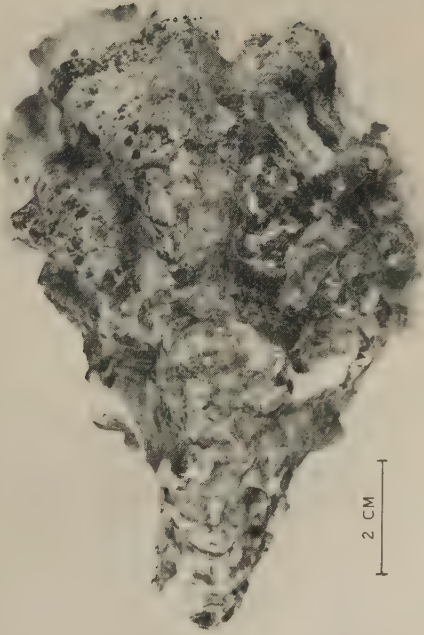
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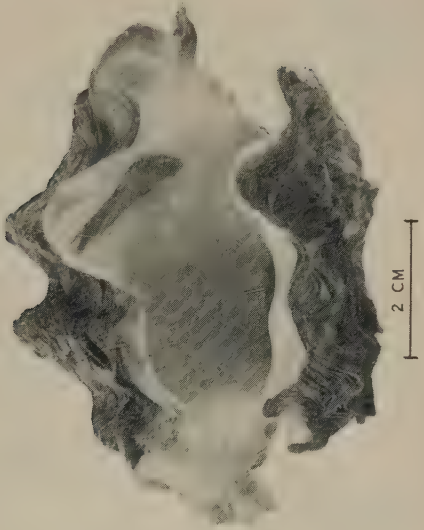
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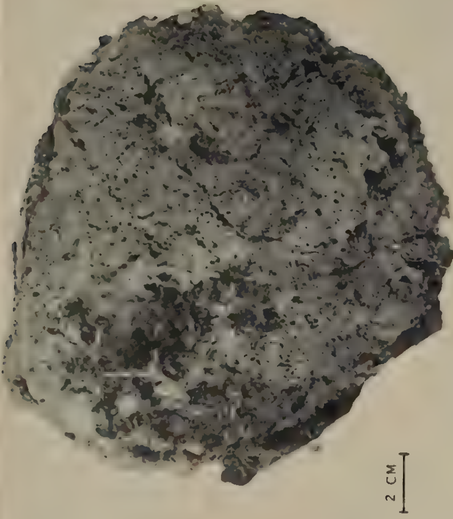
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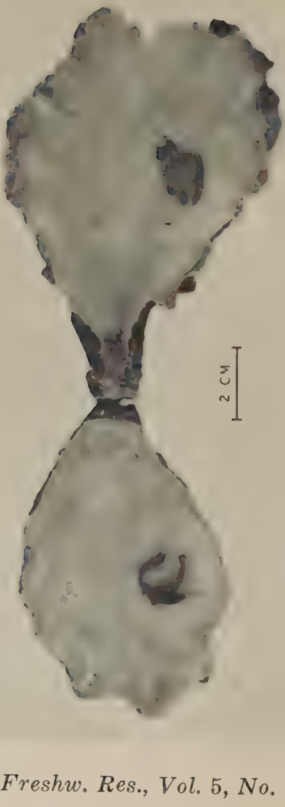
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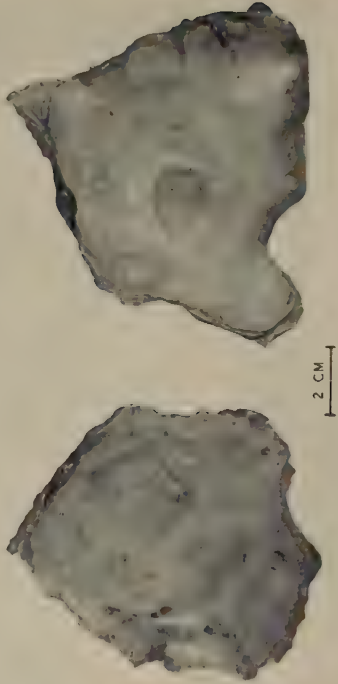
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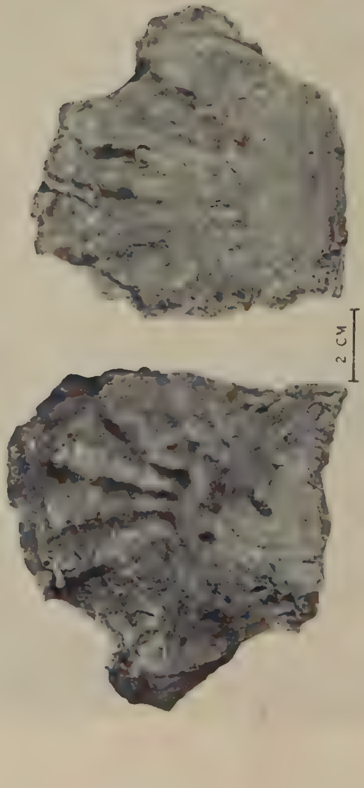
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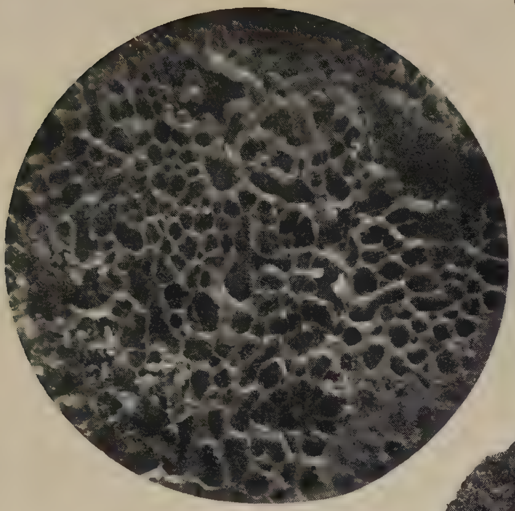

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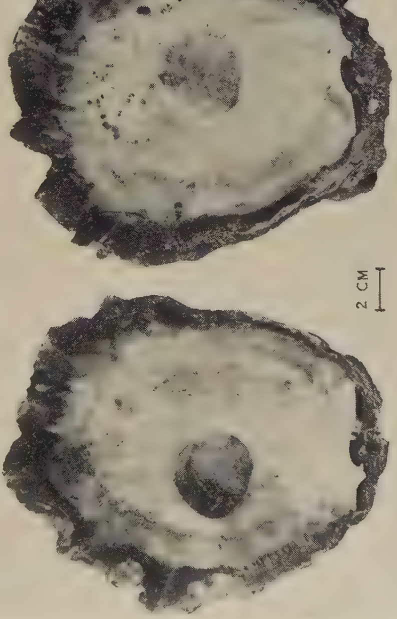

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CORRIGENDA

VOLUME 4, NUMBER 2

Pages 228 and 232, in the explanations of Figures 1 and 3: For *Petroscirtes anolius* read *Omobranchus anolius.*

Facing page 291, Plate 2, Figure 1: The left-hand scale was taken at recovery, that on the right at release.

DINOFLAGELLATES IN THE AUSTRALIAN REGION

By E. J. F. Wood*

(*Manuscript received May 11, 1953*)

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Summary

In this paper, the taxonomy of the dinoflagellates found in Australian waters is given, and the species concept as applied to the group is discussed. It is suggested that the Linnaean species concept cannot be strictly applied to a group which has, as a whole, no known sexual process and of which the vast majority of forms has not been cultivated.

The seasonal variation and fluctuations of dinoflagellates in Australian waters are considered. It is found that, as usual, the greatest number of species occurs in warmer waters.

Dinoflagellates are regarded as excellent indicators of water masses, and in one example, i.e. west of Tasmania, subtropical dinoflagellates led to the postulation of a subtropical current flowing east from Cape Leeuwin to King I. This has recently been confirmed by the finding of warm-water turtles on the west coast of Tasmania.

Dinoflagellates are not as important as diatoms or tropical blue-green algae in productivity, except on rare occasions, but do serve as food for certain groups, e.g. salps, tintinnids, etc. Some are holophytic, some holozoic, and some facultative.

No single factor or set of factors can be adduced to explain dinoflagellate maxima. There is some evidence of a rhythm, which may be tidal, in *Goniaulax digitale* and also in *G. catenella*.

I. INTRODUCTION

This study of dinoflagellates in Australian waters was begun as part of the plankton programme of the Division of Fisheries, C.S.I.R.O. The object of the work was to find indicator species which would assist the Division in following, and later possibly predicting, the movements of fish. It soon became evident that the first necessity was a full taxonomic study of the group, because of the similarity of a number of the forms which would be likely to serve as indicators of water movement. Accordingly, the first section of the paper deals with the taxonomy of the group, and is followed by a consideration of seasonal variation and fluctuations, and the relation of the observed dinoflagellate population to the water masses on and around the Australian coast.

There are a number of gaps in the record. Few plankton tows have been made in the middle part of the Great Australian Bight because of the prevalence of bad weather and a lack of suitable shelter for small vessels. There are not many records from northern Australia because the research vessels have mainly confined their cruises to areas where fisheries were likely, close to the more populated parts of the country, i.e. the south-east and the south-west. Only the work of Steemann Nielsen (1934) gives an indication of the dinoflagellate flora inside the Great Barrier Reef (the Low I. Expedition did not publish lists of species), while there are very few data from the Coral Sea, an important area in this type of investigation.

However, there is no likelihood of filling any of these gaps, in the near future, and the taxonomic record is probably fairly complete. The general ecological picture is also reasonably clear. Fortunately, workers in other ecological fields of marine biology in Australia have also reached a stage where publication of their findings is desirable, and the author has been able to discuss his results with these workers. There is a strong correlation between the regions of distribution of dinoflagellates and of euphausids as found by Sheard (unpublished data), and both Sheard's regions and the author's agree well with those demarcated by Bennett and Pope (1953) in their studies on shore-line ecology.

Because dinoflagellates are transported by currents and because different forms occur at different times and under different conditions, they are a peculiarly useful group for use as indicators of the movement of water masses. They do not, except in estuaries or on rare occasions in the sea, make up a large part of the biomass, and even then it is doubtful whether they are used directly in the food chain. Evidence of this will be given later in this paper.

The material studied includes collections by Fisheries Research Vessels, *Warreen, Stanley Fowler, Liawenee, Fairwind,* and *Derwent Hunter,* in the course of the programme of the Division of Fisheries, and other collections by Dr. D. L. Serventy and Mr. K. Sheard in Western Australia, Mr. M. Olsen in Tasmania, Mr. I. Munro and Mr. J. Thomson in Moreton Bay, Queensland, Mr. S. Hynd at Thursday I., and by the author and his staff at Cronulla. The Danish Research Vessel *Galathea* very kindly made collections from the Coral Sea for the purpose of this work, and the British Australian New Zealand Antarctic Research Expedition (B.A.N.Z.A.R.E.) phytoplankton collections and the Low I. plankton collection of the Great Barrier Reef Expedition were also made available.

In addition, Dr. M. Parke and Professor T. Braarud sent material for direct comparison of the European forms with those of this hemisphere. The author is very grateful for this invaluable assistance. The tabulated data from which the results of this study were compiled are available at the Division of Fisheries, C.S.I.R.O., Cronulla, N.S.W.

II. TAXONOMY

(*a*) *Taxonomic Considerations*

The taxonomy of the dinoflagellates presents many of the difficulties that we find in the bacteria. In neither group is there any known sexual process, so it is impossible to provide a phylogenetic classification in the true Linnean sense. In neither group is there a fixed and unalterable type specimen with which subsequent organisms can be compared. We are thus faced with the necessity of comparing our organisms with the diagrams and descriptions by previous authors, and descriptions of the earlier authors are incomplete or hard to follow. Sometimes, e.g. Kofoid and Michener (1911), descriptions were published without diagrams and it is the author's contention that such descriptions should be regarded as *nomina nuda*. Schiller (1937) has done this with *Peridinium* but not in *Goniaulax*.

The mode of nutrition is of little use in taxonomy because, as in the bacteria, some species of a genus may be heterotrophic (holozoic) while others are autotrophic (holophytic), and the same species may be holophytic or holozoic under different conditions.

Like the bacteria, too, the dinoflagellates are unicellular and exhibit a great deal of variation in morphology. The environment can act much more directly on a single independent cell than on a cell which shares with other cells the functions necessary for a complex organism. Thus the environment can select phenotypes and genotypes for survival. This means that in changed environments the population can be made up of different variants of a species or of closely related species so that it is not possible to tell by a study of populations which are species and which are eco-forms, especially in the absence of a sexual phase.

This accounts for the disagreement by competent planktologists on the identity of species among the dinoflagellates and brings us to a consideration of the species concept in this group. The author has discussed in a previous paper (Wood 1950) the genus-species concept in the bacteria, and agreed with van Niel (1946) that genus and species in that group cannot have a Linnean significance. The same applies to the dinoflagellates because of the absence of a sexual process. Paulsen (1949) recognized this and states, "Now, as we know, 'species' is a difficult concept. Among the higher plants the best definition is perhaps: species is the name given to two forms that are mutually sterile; or better, whose mutual offspring are sterile. But as the dinoflagellates are asexual (as far as we know) and moreover variable, we cannot actually speak of their speciès. Accordingly, we might well ask the question: which deviations from a main form are merely phenotypic, which are genotypic? Or in other words, are the forms and varieties . . . direct results of exterior influences, or may some of them be due to a genotypic change in the nature of the organism, possibly induced by exterior conditions but now constant and thus now a new biotype?"

So far, despite attempts by various workers, including the author, it has not been found possible to cultivate the truly oceanic dinoflagellates, so it is not possible to study the effect of environment on them. The ubiquitous *Ceratium* species, *C. tripos, C. furca,* and *C. fusus, Prorocentrum micans,* etc. have recently been cultured by Braarud and co-workers but the frequency of aberrant forms in these cultures suggests that present culture methods are of limited value in solving taxonomic problems (Hasle and Nordli 1951). Steemann Nielsen (1934) and Bohm (1931) have used size measurements to differentiate certain species of *Ceratium,* e.g. *C. tripos, C. pulchellum,* and *C. tripodioides,* but one would not consider doing so in *Goniodoma.* The author has found that frequently a given size-group is dominant in any one catch, but when the same species, e.g. *Goniodoma,* varies in size in a catch, two distinct size-groups occur, representing, no doubt, different generations of the same species. It does not seem logical, therefore to use size as a differential character, or if it is used it must be used with caution, with other factors taken into consideration.

Most of the species considered in this paper are either tropical or eurythermic, and many of them have been described from one or a few examples so that the range of variation is unknown. This gives a tendency to create species on the basis of morphological differences, which may or may not be of taxonomic significance. A case in point is the genus *Histioneis* in which many of the species have been seen only once. The descriptions given in this paper are compiled from various authorities. Where possible, the original author has been consulted. However, most of the earlier descriptions lack the essential features now regarded as characteristic of the species. For this reason one is forced to accept descriptions by Schiller and other more recent workers, and at times adapt even these to fit the organisms, e.g. in Paulsen's (1949) modification of Schiller's (1937) classification of *Peridinium.* Thus the descriptions have been brought up to date as far as possible. For detailed synonymy, the reader is referred to Kofoid and Skogsberg (1928) for the Dinophysidae and to Schiller (1933, 1937) for the rest of the dinoflagellates.

The illustrations have been taken from actual specimens found in this investigation, some being camera lucida drawings, and some drawn from photographs.

(*b*) *Classification*

The dinoflagellates belong to the class Mastigophora Diesing, subclass Dinoflagellata, characterized by the possession of 2 flagella, 1 of which is transverse. They are predominantly holophytic, usually possess chromatophores, and many are conspicuously coloured, brown, green, or orange. The body is covered by an envelope which is often sculptured (panzer).

Typically, the order is characterized by the presence of a girdle, annulus, or transverse furrow, which divides the body into an epicone and hypocone, and of a sulcus or longitudinal furrow running from the girdle to the base of the hypocone, and often extended towards or to the apex of the epicone. If the cell is armoured, the portion of the shell anterior to the girdle is the epitheca, and the posterior part, the hypotheca. The transverse flagellum (rarely seen in preserved specimens) emerges at the junction of girdle and sulcus (anterior flagellar pore) and runs round the body. The longitudinal flagellum emerges from the posterior flagellar pore situated in the sulcus portion of the hypocone, and projecting posteriorly.

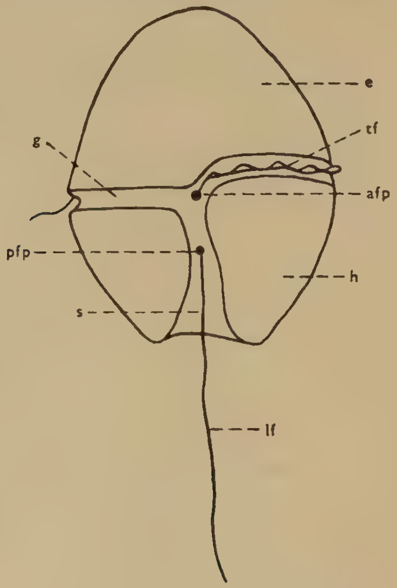

Fig. *A*.—Diagram of typical naked dinoflagellate. *e*, Epicone; *h*, hypocone; *g*, girdle; *s*, sulcus; *tf*, transverse flagellum; *lf*, longitudinal flagellum; *afp*, anterior flagellar pore; *pfp*, posterior flagellar pore. (After Lebour.)

There is usually a single large nucleus, 2 types of vacuole, one type large, connected by a canal with the flagellar pore and known as a pusule, the other type small. A stigma is often present in freshwater forms and the Pouchetiidae possess an ocellus. Chromatophores are usually small and numerous.

Reproduction is asexual by binary or multiple fission or budding; encystment is frequent: conjugation has been reported by Diwald (1946) for certain forms, but has not been confirmed except perhaps in *Noctiluca.*

In some genera, e.g. *Pyrocystis*, the common form does not resemble the above description. However, reproduction has been observed in most of them, by means of *Gymnodinium*-type spores which are morphologically indistinguishable from those of *Goniaulax* or from the genus *Gymnodinium.*

After consideration of the taxonomic studies that have been made on this group, the author has reached agreement with Paulsen (1949) that Lebour's (1925) groupings are the most clearly defined, the simplest, and most useful. They will therefore be followed with the addition of 3 families, Heterodiniidae (Kofoid), to include *Heterodinium* and *Centrodinum,* Ceratiidae to include *Ceratium,* and Dinococcidae (Pascher) to include *Pyrocystis, Cystodinium,* etc.

The Dinoflagellata are divided into 2 orders:

- Order Adiniferidea Kofoid and Swezy
    - Thecatoidae Kofoid and Swezy
    - Family Prorocentridae Kofoid
- Order Diniferidea Kofoid and Swezy
    - Family Pronoctilucidae Lebour
    - Family Gymnodiniidae Kofoid
    - Family Polykrikidae Kofoid and Swezy (emend Lebour)
    - Family Noctilucidae Saville-Kent
    - Family Pouchetiidae Kofoid and Swezy
    - Family Blastodiniidae Kofoid and Swezy
    - Family Dinococcidae (Pascher)
    - Family Dinophysidae Kofoid and Michener
    - Family Glenodiniidae Lebour
    - Family Peridiniidae Kofoid
    - Family Heterodiniidae Lindemann
    - Family Ceratiidae

Some rearrangement of genera in the families has been thought desirable. *Hemidinium* has been transferred from the Gymnodiniidae to the Glenodiniidae and *Pyrophacus* has also been assigned to the Glenodiniidae, following Schiller. The genera *Peridiniopsis, Entzia, Diplopsalopsis,* and *Minuscula* have been dropped, following the suggestion of Paulsen (1949). *Diplopsalis* has been retained (Schiller 1937; Paulsen 1949) and placed with the Peridiniidae.

(c) *Detailed Taxonomy*

Order **ADINIFERIDEA**

Family **PROROCENTRIDAE** Kofoid

Genus EXUVIAELLA Cienkowski

Exuviaella Cienkowski, 1881.

Subspherical or oval; no anterior projection except 2 flagella; 2 lateral chromatophores large, brown, each with pyrenoid and starch body; nucleus posterior; salt water. Type species *E. marina* Cienkowski.

EXUVIAELLA MARINA Cienkowski

Fig. 1

Exuviaella marina Cienkowski, 1881.

Cryptomonas lima Ehrenberg, 1873.

Dinopyxis laevis Stein, 1883.

Exuviaella lima (Ehr.) Butschli, 1885, Paulsen, 1908 partim.

E. laevis (Stein) Schröder, 1900.

Cell oval, broadest behind the centre, much compressed laterally. Front end indented in both valves, without spines. Theca with fine scattered poroids. Two large, yellow, plate-like chromatophores with a pyrenoid in the centre of each. Nucleus posterior. Length 36-50 μ. May have a fixed resting stage attached to algae by a stalk. Division may take place in a thin cyst.

Distribution.—Neritic, littoral. Europe and east coast of America. Australia: Port Hacking, N.S.W.; Western Australia.

EXUVIAELLA COMPRESSA (Bailey & Ostenfeld)

Fig. 2

Exuviaella compressa (Bailey & Ostenfeld), 1903.

Pyxidicula compressa Bailey, 1851.

Exuviaella marina Schütt, 1895, 1896.

Dinopyxis compressa Stein, 1883.

Prorocentrum bidens Schiller, 1928.

Cell oval, not much compressed. Each valve with a very small tooth near the exit of the flagella. Theca covered with conspicuous poroids. Two plate-like yellow chromatophores.

Distribution.—Oceanic form. In all European seas except the Baltic and the inner North Sea. Mediterranean; Atlantic; Pacific Ocean. Australia: Jibbon Station, Port Hacking; common in Broken Bay, N.S.W.; Fremantle,-W.A. (Schröder 1906).

Genus PORELLA Schiller

Porella Schiller, 1928.

PORELLA PERFORATA Gran

Fig. 3

Porella perforata Gran, 1915.

Cell a rounded oval, flattened laterally. In the centre of each valve is a cone-like indentation facing inwards, with a row of poroids round the margin. One valve with 2 pores, presumably for exit of flagella, borne on a small projection which fits into an excavation in the corresponding valve. Two yellow-brown chromatophores. Nucleus posterior, 22-27 by 18-21 μ. In older specimens the margins of the valves are striated. Very minute, tooth-like processes may occur at the anterior end.

Distribution.—Mediterranean, North Sea, English Channel. Australia: Jibbon Station, Port Hacking, N.S.W., very rare.

Genus PROROCENTRUM Ehrenberg

Prorocentrum Ehrenburg, 1883.

Elongate oval; anterior end bluntly pointed with spinous projection at pole; chromatophores small, yellowish brown; salt water. Type species *P. micans* Ehr. (Syn. *Cercaria* Michaelis 1830).

Section *Postprorocentrum* Gourret, 1883.

PROROCENTRUM SCUTELLUM Schröder

Fig. 4

Prorocentrum scutellum Schröder, 1901.

Cell broadly heart-shaped, slightly indented in front, with a distinct spine on the left valve with an extremely thin wing, the after end very slightly pointed or rounded. Pores numerous, of varying size, sometimes slightly spiny.

Distribution.—Atlantic coasts; Mediterranean; Gulf of Siam; India; Japan; Australia: Port Hacking, N.S.W., not common.

PROROCENTRUM MICANS Ehrenberg

Fig. 5

Prorocentrum micans Ehrenberg, 1833.
Cercaria Michaelis, 1830.

Cell strongly compressed laterally, broadest about the middle, somewhat heart-shaped. Dorsal side more convex than the ventral, and bearing a solid tooth only developed on the left valve and provided with a winglike membrane. A posterior spine has been reported by Gran and Braarud (1935), but was not seen in this material. Surface with numerous pores, often regularly arranged. Length 36-48 μ without spine. Megacytic forms occur.

Distribution.—Neritic, estuarine, and oceanic. Probably world-wide. Australia: Jervis Bay, N.S.W., to New Guinea, Storm Bay, Tas.; South Australia, Swan River, W.A.; common. In Australian waters this species varies greatly in size and shape, suggesting that *P. schilleri, P. gibbosum,* and *P. triestinum* are probably forms of *P. micans.* Braarud and Rossavik (1951) recorded a corresponding morphological variation in culture and suggested the identity of several species.

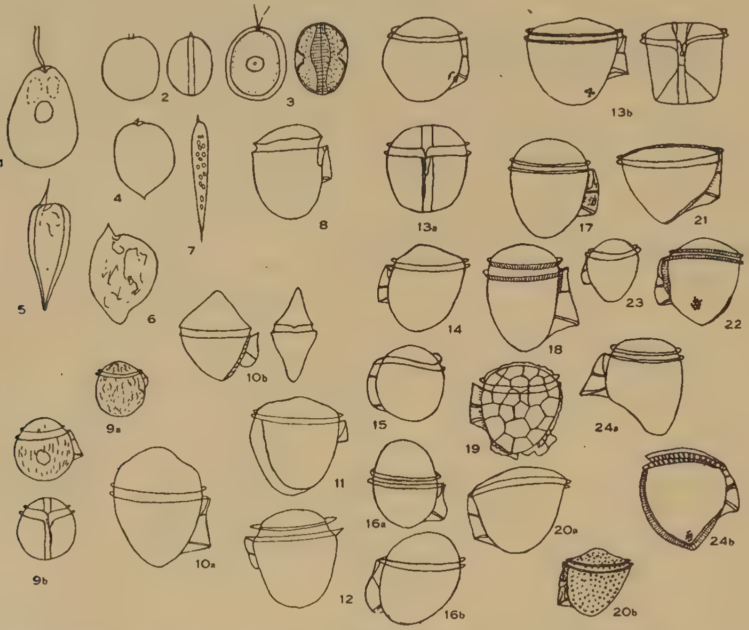

Fig. 1.—*Exuviaella marina* Cienkowski, 1881. Port Hacking. Fig. 2.—*E. compressa* (Bailey & Ostenfeld), 1903. Port Hacking. Fig. 3.—*Porella perforata* Gran, 1928. Port Hacking. Fig. 4.—*Prorocentrum scutellum* Schröder, 1901. Port Hacking. Fig. 5.—*P. micans* Ehrenberg, 1883. Port Hacking. Fig. 6.—*P. dentatum* Stein, 1883. Port Hacking. Fig. 7.—*P. rostratum* Stein, 1883. Sydney Harbour. Fig. 8.—? *Pseudophalacroma nasutum* (Stein) Jörgensen, 1923. This form has the characters of *Pseudophalacroma,* but does not entirely agree with the sketches of *P. nasutum* drawn by Stein. Fig. 9.—*a, Phalacroma pulchellum* Lebour, 1925. Port Hacking; *b, P. pulchellum.* B.A.N.Z.A.R.E. FSN5*A* (south of Tasmania). Fig. 10.—*a, P. apicatum* Kofoid & Skogsberg, 1928. Jibbon Cape; *b, P. apicatum.* B.A.N.Z.A.R.E. St. 114. Fig. 11.—*P. irregulare* Lebour, 1925. Off Eden. Fig. 12.—*P. lens* Kofoid & Skogsberg, 1928. Garden I. Sydney Harbour. Fig. 13.—*a, P. rudgei* Murray & Whitting, 1899. Port Hacking; *b, P. rudgei?* Port Hacking. Fig. 14.—*P. operculatum* Stein, 1883. Port Hacking. Fig. 15.—*P. porosum* (Kofoid & Michener) Kofoid & Skogsberg, 1928. Antarctic (B.A.N.Z.A.R.E.). Fig. 16.—*a, P. argus* Stein, 1883. Trial Bay; *b, P. argus.* Trial Bay. Fig. 17.—*P. ovum* Schütt, 1895. Trial Bay. Fig. 18.—*P. elongatum* Jörgensen, 1923. Trial Bay. Fig. 19.—*P. mawsonii* sp. nov. Antarctic convergence (B.A.N.Z.A.R.E.). Fig. 20.—*a, P. cuneus* Schütt, 1895. Trial Bay; *b, P. cuneus.* Eden. Fig. 21.—*P. triangulare* sp. nov. Trial Bay. Fig. 22.—*P. acutum* (Schütt) Pavillard, 1916. Fig. 23.—*P. minutum* Cleve, 1900. Trial Bay. Fig. 24.—*a, P. rapa* Stein, 1883. Port Hacking; *b, P. rapa.* Trial Bay.

PROROCENTRUM DENTATUM Stein

Fig. 6

Prorocentrum dentatum Stein, 1883.

Cell oval, pointed at posterior end, broadest in front of the centre. Both valves similar, each bearing a 3-cornered, hollow, tooth-like process, which together form the dorsal horn.

Distribution.—Oceanic; Atlantic; North Sea; Mediterranean. Australia: Jibbon Station, Port Hacking, N.S.W.

PROROCENTRUM ROSTRATUM Stein

Fig. 7

Prorocentrum rostratum Stein, 1883.
P. stylifer Lohmann, 1920.
P. tenue Lohmann, 1920.

Cell elongate, about 5-6 times as long as broad. Dorsal side wavy and both valves ending in a long thin process which in valve view is pointed, in suture view notched or flat at end. Sagittal view wedge-shaped.

Distribution.—Atlantic; Mediterranean; Australia: Sydney Harbour, N.S.W.

Order DINIFERIDEA

Family **DINOPHYSIDAE** Kofoid and Michener

Body flattened laterally; theca divided by a seam (suture) into 2 lateral halves. Girdle usually anterior, never postmedian; epitheca usually low: girdle and sulcus with wings or "lists" on each side, often supported by ribs or spines: no apical pore: theca usually porulate.

KEY TO GENERA OF THE FAMILY DINOPHYSIDAE

1.	Left sulcal list very slightly developed, without ribs or spines	*Pseudophalacroma*
	Left sulcal list well developed, with at least 2 ribs	2
2(1).	Epitheca projecting beyond anterior girdle list	*Phalacroma*
	Epitheca not so projecting	3
3(2).	Anterior girdle list stalked	4
	Anterior girdle list not stalked	5
4(3).	Posterior angular list with submarginal cross rib	*Histioneis*
	Posterior angular list without submarginal rib	*Parahistioneis*
5(3).	Body greatly elongated, with 1 or 2 antapicals	6
	Body not greatly elongate	8
6(5).	Theca hyaline or slightly sculptured	7
	Theca sculpture porulate or reticulate	*Dinophysis*
7(6).	One antapical process, which may be branched at antapex	*Amphisolenia*
	Two antapical processes	*Triposolenia*
8(5).	Anterior girdle list not more than $\frac{1}{4}$ width of body	*Dinophysis*
	Anterior girdle list 0.4-1.5 times width of body	9
9(8).	Posterior girdle list with submarginal cross rib	*Histioneis*
	No cross rib on posterior girdle list	10
10(9).	Posterior girdle list with less than 6 radial ribs	*Parahistioneis*
	Posterior girdle list with more than 6 radial ribs	*Ornithocercus*

Genus PSEUDOPHALACROMA Kofoid & Skogsberg

Pseudophalacroma Kofoid & Skogsberg, 1928.

Epitheca conspicuous: sulcus prolonged onto epitheca up to about 2/3 the distance from girdle to apex, showing a dilated, rounded end; left longitudinal list very slightly developed and presumably destitute of ribs or spines. Type species *P. nasutum* Jörgensen.

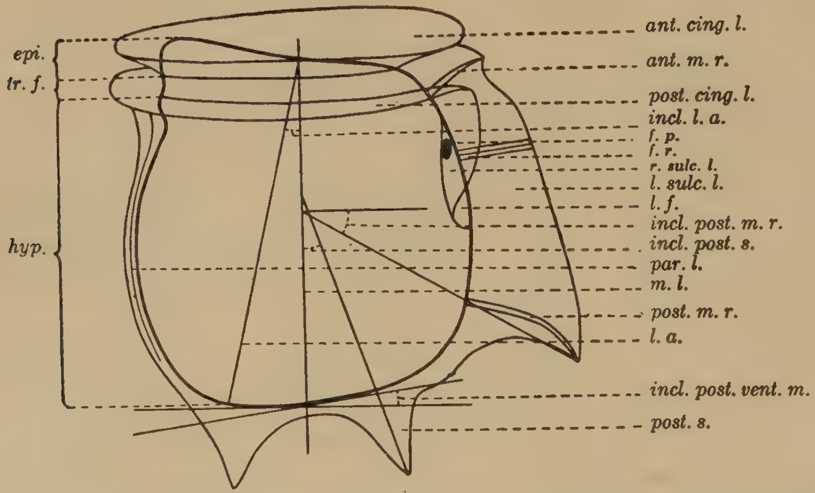

Fig. *B.—Dinophysis collaris* Kofoid and Michener, right lateral view. Terminology and methods of making measurements of *Phalacroma* and *Dinophysis*. Terminology.—The midline is the perpendicular to girdle which is equidistant from dorsal and ventral margins of body at place of greatest depth of body. When longitudinal axis of body is not inclined, it coincides with midline. In specimen represented the longitudinal axis of body is inclined *posterodorsally* and the posteroventral margin of body *dorsoposteriorly*, according to our terminology. The anterior main rib (R_1) is the rib at junction of left sulcal list and posterior cingular list. The fission rib (R_2) is the rib of left sulcal list at place where this list is divided in binary fission. The posterior main rib (R_3) is the rib of left sulcal list near posterior end of this list or, if two or more ribs in this region, the best developed of these. Ventral margin of left sulcal list is the free edge of this list between R_1 and R_3; posterior margin of this list is the free edge behind R_3 (after Kofoid and Skogsberg).

? PSEUDOPHALACROMA NASUTUM (Stein) Jörgensen

Fig. 8

Pseudophalacroma nasutum (Stein) Jörgensen, 1923.
Phalacroma nasutum Stein, 1883; Entz, 1905.

Body in lateral view rounded oval. Epitheca low and small. Girdle lists poorly developed. Groove somewhat constricted; sulcal list (left) poorly developed, stronger than right, reaching to the middle of hypotheca. Body in ventral view elliptical with rounded ends. Theca with rather large, crowded, grain-like areoles 40-50 by 40-44 μ.

Distribution.—Mediterranean, Florida currents, Atlantic Ocean. Norwegian coast near Bergen, often in great depths. One example from

Port Hacking, N.S.W., and 1 from Eden have been referred to this species.

Genus PHALACROMA Stein

Phalacroma Stein, 1883.

Body usually not so compressed laterally as in *Dinophysis*. Epitheca rising above transverse lists, which are not conspicuous and are uniformly developed. Chromatophores usually absent. Type species *P. porodictyum* Stein.

Key to Species of the Genus Phalacroma Described in this Paper

1.	Sulcus extending into epitheca	*P. pulchellum*
	Sulcus not extending into epitheca	2
2 (1).	Body circular to subcircular	3
	Body diamond-shaped	*P. apicatum*
	Body more or less cuneate in lateral view	14
3 (2).	Body with antapical process but no spine	*P. hindmarchii*
	Body without antapical process	4
4 (3).	Body with toothed extensions of both valves at suture	*P. mawsonii*
	Body with posterior sail but no dorsal extension	*P. doryphorum*
	Body with 3 posterior sails and dorsal sail	*P. jibbonense*
	Body with no posterior sail, dorsal sail present, beginning at girdle list	*P. alata*
	Body with posterior sail with dorsal extension	5
	Body with no posterior sail	6
5 (4).	Dorsal extension of posterior sail with margin indentate	*P. thompsonii*
	Dorsal extension of posterior sail with entire margin to girdle	*P. pulchrum*
6 (4).	Girdle slightly anterior to midline	7
	Girdle strongly anterior	8
7 (6).	Cell elliptical, epitheca semicircular	*P. argus*
	Cell elliptical, epitheca slightly domed	*P. operculatum*
	Cell oval, epitheca domed	*P. apicatum*
8 (6).	Girdle depressed, narrower anteriorly	*P. lens*
	Girdle not depressed	9
9 (8).	Body rotund, little compressed laterally	10
	Body oval, more or less compressed	12
10 (9).	Girdle sigmoid	*P. porosum*
	Girdle straight or slightly curved	11
11(10).	Left sulcal list ending about ½ way to antapex	*P. irregulare*
	Left sulcal list extending about ¾ way to antapex	*P. rudgei*
12 (9).	Epitheca low: body elongate oval	*P. elongatum*
	Epitheca prominent: body oval	13
13(12).	Body oval in sagittal view	*P. ovum*
	Body wedge-shaped in sagittal view	*P. minutum*
14 (2).	Body wedge-shaped in lateral view	15
	Body trapezoidal	17
15(14).	Body evenly convex between R_3 and antapex	16
	Body with sharp angle at R_3	*P. acutum*
16(15).	Left sulcal list not reaching antapex	*P. cuneus*
	Left sulcal list reaching antapex	*P. triangulare*
17(14).	Antapex rounded with slight convexity between R_3 and antapex	*P. dolichopterygium*
	Antapex with slight or definite process	18

18(17). Dorsal margin slightly concave or straight 19
Dorsal margin convex 20
19(18). Antapex making acute angle at dorsal margin .. .. *P. rapa*
Small but distinct process, dorsal margin concave at junction of process and body .. .. *P. whiteleggei*
20(18). Dorsal margin not concave .. .. *P. mitra*
Dorsal margin convex, then concave; large distinct process .. .. .. *P. favus*

Contractum group

PHALACROMA PULCHELLUM Lebour

Fig. 9

Phalacroma pulchellum Lebour, 1925.

Body rotund, very slightly flattened. Epitheca conspicuous. Girdle broad, deeply impressed, with narrow lists. Sulcus extending into the epitheca, the left longitudinal list extending about ½ way down the hypotheca, with conspicuous spines. Theca covered with small poroids, pores not apparent. Plasma pink to colourless. Megacytic forms with large fat globules and sculptureless median band frequent. Length 21-33 μ.

Distribution.—Plymouth Sound. Australia: Port Hacking, N.S.W.; Antarctic convergence (B.A.N.Z.A.R.E.).

Rotundatum group

PHALACROMA APICATUM Kofoid & Skogsberg

Fig. 10

Phalacroma apicatum Kofoid & Skogsberg, 1928.
Phalacroma sp. Okamura, 1907.

Body in side view irregularly ovate or rhombic, with a conical epitheca, widest at or slightly behind the girdle. Length 1.24-1.30 times breadth. In ventral view biconical with rounded ends, broadest at girdle, 1.4 times as long as broad. Lower girdle list about ⅓-½ way from apex. Lists like those of *P. argus*.

Distribution.—Tropical and subtropical Pacific. Australia: off Jibbon Point, Port Hacking, N.S.W.

PHALACROMA IRREGULARE Lebour

Fig. 11

Phalacroma irregulare Lebour, 1925.

Like *P. rotundatum*, but with an elongated, somewhat wedge-shaped hypotheca. Epitheca low, not covered by girdle lists. Left longitudinal list reaching about ½ way down hypotheca, with conspicuous spines. Theca with poroids each containing a pore, thus differing from those of *P. rotundatum*. Length 55-56 μ. Megacytic forms always seen, or those which have just divided, with part of the border, which has a structure of fine poroids attached. Plasma colourless to pinkish.

Distribution.—Plymouth Sound. Not common. Australia: south coast, rare.

PHALACROMA LENS Kofoid & Skogsberg

Fig. 12

Phalacroma lens Kofoid & Skogsberg, 1928.

A rather small species with body subrotund in lateral outline, somewhat constricted at girdle, and deepest just behind girdle, or in the middle. In dorsal view lens-shaped, widest in the middle, constricted anteriorly. Epitheca moderately elevated above girdle, almost evenly convex, and highest in centre. Girdle somewhat concave. Dorsal margin of hypotheca evenly and gently or moderately convex, post margin broadly and evenly convex. Ventral margin evenly convex as dorsal margin. Left sulcal list about ½ as long as body, ribs moderately strong. Theca wall finely areolate with scattered pores.

Distribution.—Tropical Pacific. Australia: east coast, Port Jackson, N.S.W.; Swan River, W.A.

PHALACROMA RUDGEI Murray & Whitting

Fig. 13*a*, *b*

Phalacroma rudgei Murray & Whitting, 1899.

Body in side view almost circular, contour of hypotheca continuous with that of epitheca. Girdle and sulcal lists narrow, the latter with small spines. In ventral view body is rotund, base and apex flattened. Theca smooth or finely areolate, length about 75 μ.

Distribution.—Subtropical Atlantic species, in Mediterranean and Adriatic. Rare in North Sea. Australia: east coast, Port Hacking, N.S.W.

PHALACROMA OPERCULATUM Stein partim

Fig. 14

Phalacroma operculatum Stein, 1883 partim.

Body in side view somewhat biconical. Epitheca much smaller than hypotheca, with straight or somewhat concave contour. Hypotheca dorsally strongly convex, almost straight along the sulcal list, then somewhat convex, tapering into the bluntly conical antapex. Girdle lists moderate, ribbed. Right and left sulcal lists strongly developed. Theca areolate, areolations containing pores.

Distribution.—Adriatic; Atlantic. Cold-water form. Australia: Port Hacking, winter form, rare.

PHALACROMA POROSUM (Kofoid & Michener) Kofoid & Skogsberg

Fig. 15

Phalacroma porosum Kofoid & Skogsberg, 1928.
P. porosa Kofoid & Michener, 1911.

Body in lateral view rounded, sometimes blunt anteriorly, somewhat wider above than below, deepest at or just behind girdle. Length 0.99-1.12 width. Narrowly ovate in ventral view. Lower girdle list 0.2-0.26 of body length from apex. Girdle makes a sigmoid curve across the side of the body. Girdle lists sometimes slightly curved upwards, not ribbed. Left sulcal list 0.52-0.65 body length. Hypotheca finely reticulate. 47-73.5 by 43.5-65.9 μ.

Distribution.—Eastern tropical Pacific to Antarctic (B.A.N.Z.A.R.E).

Argus group

PHALACROMA ARGUS Stein

Fig. 16*a*, *b*

Phalacroma argus Stein, 1883.
Phalacroma argo Hensen, 1911.

Body somewhat oval in lateral view, deepest at or somewhat behind girdle. In ventral view obovate, widest somewhat behind girdle. Posterior list $\frac{1}{4}$-$\frac{1}{2}$ way from apex to antapex. Epitheca and hypotheca rounded, hypotheca narrowing somewhat. Girdle lists may be ribbed. Left sulcal list about $\frac{1}{2}$ body length, convex to junction with body, ribs weak. Right sulcal list concave. Theca reticulate, porulate; markings may be light.

Distribution.—Widely distributed in tropical and subtropical waters. Australia: south-east coast of New South Wales from Trial Bay to Eden in water of the east Australian current, and in deep water south-west of Port Fairy, Vic., west of Bass Strait.

PHALACROMA OVUM Schütt

Fig. 17

Phalacroma ovum Schütt, 1895.
?*P. operculatum* Stein, 1883.
?Forti, 1922 partim. Non Schütt, 1895; non Jörgensen, 1923.
P. operculoides Schütt, 1895 partim. Okamura, 1912; Jörgensen, 1923; non Cleve, 1899; nec Lohmann, 1902; nec Forti, 1922.

Body ovate in lateral outline, deepest at or somewhat behind girdle. In dorsal view, narrowly obovate. Epitheca prominent, usually very convex. Hypotheca symmetrical or slightly inclined ventrally, may be oval-wedge shaped or regularly oval, convex. Posterior portion of body strikingly narrower than anterior. Girdle not depressed, lists apparently without spines. Right sulcal list extends beyond fission rib. Left sulcal list of moderate length, narrow anteriorly, wide posteriorly, straight or slightly concave, sometimes sigmoid.

Distribution.—Widely distributed in tropical, subtropical, and warm water. Australia: east coast, Eden to Trial Bay, N.S.W.

PHALACROMA ELONGATUM Jörgensen

Fig. 18

Phalacroma elongatum Jörgensen, 1923.

Body in lateral view elongated oval. Epitheca broadly rounded, low, hypotheca long, narrowly rounded below. Epitheca less than $\frac{1}{4}$ hypotheca in height. Hypotheca widest below girdle. Girdle not depressed, lists supported by rather strong spines. Left sulcal list short, reticulate, not ½ a hypotheca long (illustration shows what is obviously only portion of this list), margin straight. Theca strongly sculptured, more or less clearly reticulate.

Distribution.—Mediterranean, probably a deep-water form. Australia: east coast, rare.

PHALACROMA MAWSONII sp. nov.

Fig. 19

A medium-sized species; body ovate, longitudinal axis at right angles to girdle. Epitheca *c.* 1/5 body length, rounded; hypotheca evenly curved at sides with a bluntly rounded base. Girdle lists and girdle rather narrow. Left sulcal list moderately wide with straight margin from R_1 to R_3 ribbed, decurrent; R_2 curved forward, R_3 backward, clavate. Toothed parasagittal ridges running round from base of sulcal list to girdle list and also extending over epitheca. This form differs from *P. spinatum* Peters and *P. cornutum* Peters in its body shape, relatively narrow left sulcal list, small R_3, and shorter toothed ridges.

Distribution.—Antarctic convergence (B.A.N.Z.A.R.E.).

Cuneus group

PHALACROMA CUNEUS Schütt

Fig. 20*a*, *b*

Phalacroma cuneus Schütt, 1895.
Ph. mitra Oltmanns, 1922 partim.
Ph. blackmanni Murray & Whitting, 1899.

A medium-sized species, body cuneate in lateral outline, with a rather low and very broadly rounded epitheca, the posterior portion of the hypotheca fairly broadly to rather narrowly rounded, with the greatest depth at girdle, and about as deep as long. In dorsal view cuneate, posterior portion of hypotheca narrowly rounded to subacute. Girdle lists about as wide as girdle. Along base of anterior list is a series of ribs anastomosing into a row of polygons, at times 2 rows. Posterior list simply ribbed. Sulcus about ½ as long as hypotheca, right sulcal list long and narrow, ending about ½ way between fission rib and posterior main rib of left sulcal list. The latter is of moderate size, margin gently sigmoid, usually irregularly striate. Theca reticulate with medium-sized polygons each with a central pore.

Distribution.—World-wide in tropical and warm-temperate waters, east Australia as far south as Eden, N.S.W.

PHALACROMA TRIANGULARE sp. nov.

Fig. 21

A large wedge-shaped species related to *P. cuneus*. Epitheca low, evenly curved. Girdle lists moderate, width about equal to girdle, hyaline.

Hypotheca obtusely wedge-shaped with rather sharp antapex. Wedge-shaped with concave sides in ventral view, left sulcal list broadly triagular with straight or slightly concave edges, ribbed: R_3 moderate, 80 by 65 μ.

Distribution.—East Australia.

Rapa group

PHALACROMA ACUTUM (Schütt) Pavillard

Fig. 22

Phalacroma acutum Pavillard, 1916.
Phalacroma vastum var. *acuta* Schütt, 1895.

Body in lateral view asymmetrical, constricted laterally. Epitheca high, evenly rounded or bluntly conical at apex. Hypotheca asymmetrical, dorsally evenly convex to antapex, ventrally straight or slightly convex along sulcus, then from main rib straight to the slightly projecting antapex. Girdle lists concave, usually weakly inclined outwards, ribbed, about as broad as girdle. Sulcus lists very strongly developed, right reaching main rib with straight or more or less concave-convex edge, left similar, wide under main rib. Theca usually sculptured, areolate, with or without pores. Chromatophores yellow, size 60-70 by 50-52 μ.

Distribution.—Mediterranean; Atlantic (Gulf Stream); Australia: Port Hacking, N.S.W., October.

PHALACROMA MINUTUM Cleve

Fig. 23

Phalacroma minutum Cleve, 1900.

Body in lateral view somewhat wedge-shaped, laterally strongly constricted. Epitheca low, flat, evenly rounded. Hypotheca narrowed posteriorly, rounded, wedge-shaped, or conical, ventrally almost straight along the wing, then concave, forming the tapering end; dorsal margin straight or slightly convex, then slightly concave, as it reaches the antapex. Widest at the posterior girdle list. Length 1.75 breadth. In sagittal view elongate oval or wedge-shaped, broadly rounded above, below, rounded to a blunt point. Length 2.2 breadth. Girdle lists narrow, sulcal lists short with insignificant spines. 50 by 25 by 40 μ (Schiller), 40 by 28 μ (Australia).

Distribution.—Subtropical, west Atlantic species carried north with the Gulf Stream. Australia: east coast, rare.

PHALACROMA RAPA Stein

Fig. 24*a*, *b*

Phalacroma rapa Stein, 1883.
Phalacroma mitra Okamura, 1907, non 1912.

Body subcuneate in lateral view; epitheca moderately convex to almost flat; posterior portion of hypotheca narrowly rounded to subacute, but not mamilliform. Ventral margin of hypotheca strikingly angular at main rib of left sulcal list, deepest at or somewhat behind girdle. In dorsal view cuneate, hypotheca very narrowly rounded to subacute posteriorly, side contours gently concave or undulating. Girdle lists ribbed, right sulcal list varying in length, usually subtriangular. Left sulcal list small to moderate, may be decurrent.

Distribution.—Widely distributed in tropical and temperate seas. Australia: Port Hacking to Trial Bay, N.S.W., on east coast. Sydney Harbour. Recorded from Sydney Harbour by Whitelegge (1891).

PHALACROMA WHITELEGGEI sp. nov.

Fig. 25*a*, *b*

Very like *P. rapa*, but with distinct posterior process. Epitheca very low, girdle lists about equal to girdle width. Hypotheca with almost straight dorsal margin, sigmoid curvature at junction with short, evenly curved process. Base contour undulate to R_3. Ventral margin undulate, dorsal view cuneate, with concave or slightly undulate margins. Right sulcal list narrow with undulate margin and accessory ribs. Left sulcal list somewhat decurrent along antapical margin, with undulate margin and accessory rib between R_1 and R_2, smaller accessory spines. R_3 strong, directed dorsoventrally, concave towards apex. Length 80 μ, breadth 75-80 μ.

Distribution.—Off Jibbon Cape and Coff's Harbour, N.S.W.

Named after Whitelegge, who listed a number of dinoflagellates from New South Wales waters.

PHALACROMA MITRA Schütt

Fig. 26

Phalacroma mitra Schütt, 1895.

Schiller (1933) considered that this species is very probably identical with *P. rapa*. It is distinguished from *P. dolichopterygium* by the greater concavity between the antapex and the posterior main rib, and the shorter left sulcal list, and from *P. acuta* by the low, flat epitheca. *P. mitra* and *P. rapa* are much confused in the literature. Kofoid and Skogsberg (1928) considered them distinct but did not describe *P. mitra*; moreover, Kofoid is a confirmed splitter. Cleve (1901) and Jörgensen (1923) united the 2 species. The writer has recorded 2 forms, one of which has a more rounded antapex and a more oblique posteroventral margin than the other. He has placed the former as *P. rapa*, the latter as *P. mitra*. Intergrades were not found. Both occur in the same area, and make their way into estuaries.

PHALACROMA FAVUS Kofoid & Michener

Fig. 27

Phalacroma favus Kofoid & Michener, 1911.
?*Phalacroma favus* Jörgensen, 1923.

P. hindmarchii Pavillard, 1916.
P. simulans Jörgensen MS., 1923.

Body subcuneate in lateral view, with very broadly rounded epitheca, and the posterior portion of hypotheca constricted, mamilliform with the ventral margin broadly rounded or somewhat angular at the posterior main rib of the left sulcal list; with the greatest width at just below

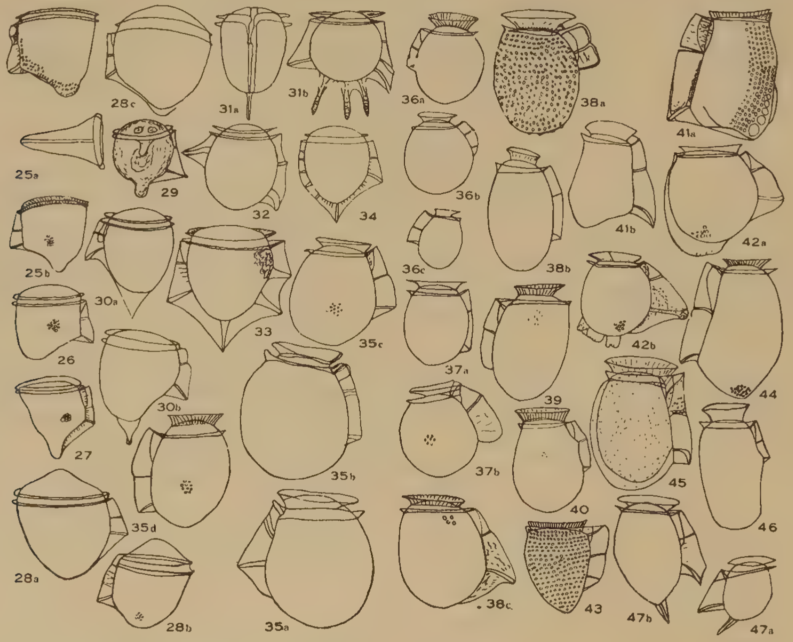

Fig. 25.—*a*, *Phalacroma whiteleggei* sp. nov. Jibbon, 1939; *b*, *P. whiteleggei*, off Coff's Harbour, 1951. Fig. 26.—*P. mitra* Schütt, 1895. Trial Bay. Fig. 27.—*P. favus* Kofoid & Michener, 1911. Trial Bay. Fig. 28.—*a*, *P. dolichopterygium* Murray & Whitting, 1899. Jibbon; *b*, *P. dolichopterygium*. Off Jervis Bay; *c*, *P. dolichopterygium*. B.A.N.Z.A.R.E. Station 77. Fig. 29.—*P. hindmarchii* Murray & Whitting, 1899. Maria I. Fig. 30.—*a*, *P. doryphorum* Stein, 1883. Trial Bay; *b*, *P. doryphorum*. Trial Bay. Fig. 31.—*P. jibbonense* sp. nov. Jibbon 1945. *a*, Ventral view; *b*, side view. Fig. 32.—*P. alata* sp. nov. Jibbon, 1942. Fig. 33.—*P. thompsonii* sp. nov. Off Port Macquarie, 1951. Fig. 34.—*P. pulchrum* (Kofoid & Michener) Jörgensen, 1923. B.A.N.Z.A.R.E. St. 114. Off Tasmania. Fig. 35.—*a*, *b*, *Dinophysis ovum* Schütt, 1895. B.A.N.Z.A.R.E. St. FSN7*a*; *c*, *D. ovum*. B.A.N.Z.A.R.E.; *d*, *D. ovum*. Port Hacking. Fig. 36.—*a*, *D. sphaerica* Stein emend Kofoid & Skogsberg, 1928. Port Hacking; *b*, *c*, *D. sphaerica*. B.A.N.Z.A.R.E. Fig. 37.—*a*, *D. arctica* Mereschkowsky, 1879. Heard I.; *b*, *D. arctica*. B.A.N.Z.A.R.E. Fig. 38.—*a*, *b*, *D. acuminata* Claparède & Lachmann, 1859. Jibbon Cape; *c*, *D. acuminata*? Antarctic, B.A.N.Z.A.R.E. St. 87. Fig. 39.—*D. similis* Kofoid & Skogsberg, 1928. Port Hacking. Fig. 40.—*D. okamurai* Kofoid & Skogsberg, 1928. Port Hacking. Fig. 41.—*a*, *D. truncata* Cleve, 1900. Storm Bay, Tasmania; *b*, *D. truncata* B.A.N.Z.A.R.E. St. 77. Tasmania. Fig. 42.—*a*, *b*, *D. tuberculata* Mangin, 1919. B.A.N.Z.A.R.E. *a*, St. FSN5*A*; *b*, St. FSN59. Fig. 43.—*D. acuta* Ehrenberg, 1839. Off Jervis Bay. Fig. 44.—*D. schroederi* Pavillard, 1909. Port Hacking. Fig. 45.—*D. fortii* Pavillard, 1923. Port Hacking. Fig. 46.—*D. sacculus* Stein, 1883. Port Hacking. Fig. 47.—*a*, *b*, *D. hastata* Stein, 1883. Trial Bay.

the girdle. Very broadly convex, girdle slightly concave, lists heavily ribbed. Right sulcal list extends to main rib of left sulcal list, which is moderate to decurrent, strongly ribbed.

Distribution.—Probably widely distributed in tropical, subtropical, and warm-temperate seas. Australia: east coast, Trial Bay, N.S.W.

PHALACROMA DOLICHOPTERYGIUM Murray & Whitting

Fig. 28*a-c*

Phalacroma dolichopterygium Murray & Whitting, 1899.

Schiller (1933, 1937) considered this species to be identical with *P. rapa* Stein. Differs from *P. acuta* in the lower, flatter epitheca and the decurrent sulcal list which reaches the antapex, from *P. mitra* in the less concave ventral contour and the antapex, and from *P. rapa* through the less angular contour at the posterior main rib.

A form somewhat resembling this species was found in Port Hacking, N.S.W. It has the decurrent left sulcal list, but has a relatively high bluntly conical epitheca and no ventral concavity in the hypotheca. It resembles *P. acutum,* also recorded from Port Hacking, but lacks the heavily ribbed sulcal region and the very heavy thecal sculpture, while it has the strongly decurrent list of *P. dolichopterygium.* A second form resembling this, but showing a slight ventral concavity, was found in plankton off the south-east coast in 1950, suggesting that it is correct to ascribe the above form to this species.

PHALACROMA HINDMARCHII Murray & Whitting

Fig. 29

Phalacroma hindmarchii Murray & Whitting, 1899.

Body in lateral view inverted fig-shape; epitheca broad and more or less strongly convex, lower part of hypotheca constricted, mamillate, ventral margin sigmoid, convex above, concave below, broadest at or somewhat behind girdle, antapex rounded. Dorsoventral and lateral views almost similar. Girdle about $\frac{1}{4}$-$\frac{1}{2}$ way from apex to antapex, lists not ribbed. Right sulcal list extends to posterior main rib of left sulcal list, width subequal. Left sulcal list moderate, ending somewhat in front of base of antapical lobe. Posterior main rib well developed, clubbed.

Distribution.—Probably widely distributed in tropical, subtropical, and warm-temperate waters. Australia: Maria I., Tas.; Eden, N.S.W.

Doryphorum group

PHALACROMA DORYPHORUM Stein

Fig. 30*a, b*

Phalacroma doryphorum Stein, 1883.

A medium-sized species. Body in lateral view more or less oval, deepest at, or somewhat behind, girdle. Epitheca evenly and moderately convex to flat, moderately or slightly elevated above girdle. Hypotheca symmetrical, of an oval wedge shape or regularly oval, posterior portion strikingly narrower than anterior. In dorsoventral view the body is narrowly obovate to cuneate. Girdle flat or slightly convex, lists without spines. Right sulcal list ends above or below posterior main rib of left sulcal list, varies in shape. Left sulcal list rather short, triangular, wide at posterior main rib. There is a posterior sail, with or without a supporting rib or reticulations either on or ventral to antapex, usually well separated from left sulcal list. Theca finely and closely areolate.

Distribution.—Widely distributed in tropical, subtropical, and warm-temperate seas. Australia: east coast, Eden to Trial Bay, also at deep station south-west of Port Fairy, to the west of Bass Strait.

Limbatum group

PHALACROMA JIBBONENSE sp. nov.

Fig. 31*a, b*

A small species with body circular in lateral view. Epitheca, girdle, and hypotheca evenly rounded. Epitheca low, girdle lists wide, ribbed. Right sulcal list extending to fission rib. Left sulcal list slightly concave in margin; posterior main rib club-shaped, list extending to dorsal side, more or less deeply indented, and supported beyond posterior main rib by 4 club-shaped spines, the last 3 echinulate. A triangular sail supported by a rib extends from posterior girdle list to near the end of the left sulcal list. Body areolate, 45 μ in diameter.

This species bears a remarkable resemblance to *Ceratocorys gourreti*, for which it was at first mistaken. It shows affinities with *Ornithocercus*. It may be that Schütt's *Phalacroma jourdăni* was really a *Phalacroma*, in which case *P. jibbonense* would be a synonym.

Distribution.—Collected off Jibbon Cape, Port Hacking, N.S.W., on 2 occasions and off the east coast in 1950.

PHALACROMA ALATA sp. nov.

Fig. 32

A medium-sized species. Body subspherical, longitudinal axis at right angles to girdle plane. Epitheca low, rounded, about equal to girdle in width. Hypotheca widest at midline. Girdle lists narrow, hyaline. Left sulcal list moderate, margin concave to fission rib, concave, then convex to R_3, which is sharply curved towards antapex, margin recurved below R_3. The species is characterized by a triangular dorsal sail beginning at girdle list, and supported by a long spine, sail margins concave, 50 by 60 by 30 μ.

Distribution.—Type specimen from Jibbon Cape, N.S.W., 17. viii. 1942.

PHALACROMA THOMPSONII sp. nov.

Fig. 33

A medium-sized species of the *limbatum* group. Rather larger than *P. jibbonense* and with a subovate body, longitudinal axis at right angles to girdle plane. Epitheca low, rounded, slightly more than girdle width in height. Hypotheca rather long, ventral contour rounded to R_2, slightly concave between R_2 and R_3, then convex with evenly rounded antapex, and evenly convex dorsal contour. Girdle lists about equal to girdle in width, ribbed. Girdle not or slightly depressed. Right sulcal list extending to R_2, margin convex; left sulcal list wide, margin straight to R_3, with a few short ribs or striae, then carried on 4 ribs, 1 posterior, the other 2 dorsal, to girdle list, forming 3 lobes. Theca reticulate with areoles. Named after Dr. H. Thompson, who pioneered systematic plankton work in Australia.

Distribution.—Type specimen from the 100-fm line off Port Macquarie, N.S.W., 17. vii. 1951.

PHALACROMA PULCHRUM (Kofoid & Michener) Jörgensen

Fig. 34

Phalacroma pulchrum (Kofoid & Michener) Jörgensen, 1923.
P. pulchra Kofoid & Michener, 1911 partim.
P. circumsutum Jörgensen, 1923 partim.

Body in lateral view almost circular, flattened above, widest near the middle. Length 0.99-1.3 width. In dorsal view narrow oval: 1.8 times longer than broad. Lower girdle list 0.2-0.25 body length from apex, epitheca sometimes barely discernible above anterior girdle list. Girdle lists somewhat inclined forwards; not ribbed. Left girdle list with straight margin to R_3. Two parasagittal lists on hypotheca, left very narrow, sometimes possibly absent; right continues left sulcal list; dorsally its maximum width is subequal to or less than $\frac{1}{2}$ width of girdle, on antapex it forms acute wedge-shaped posterior sail directed posteriorly with central rib, which may be divided at base; sail with 8-11 short riblets.

Theca finely reticulate, 51.2-52.5 μ long.

Distribution.—Tropical, subtropical, and warm-temperate seas. East coast of Tasmania (B.A.N.Z.A.R.E.).

Genus DINOPHYSIS Ehrenberg

Cell compressed laterally, never wedge-shaped; epitheca small or almost rudimentary with obliquely set girdle lists, the upper list being more or less funnel-shaped, projecting beyond epitheca, and often strengthened by radial ribs. Usually yellow chromatophores.

KEY TO SPECIES OF THE GENUS DINOPHYSIS DESCRIBED IN THIS PAPER

1.	Body with 1 or more posterior processes	2
	Body without posterior process	4
2 (1).	Body with 1 posterior process	*D. caudata*
	Body with 2 posterior processes	3
3 (2).	Second process smaller than 1st, both directed posteriorly	*D. tripos*
	Second process approximately equal to 1st, directed somewhat laterally	*D. miles*

4 (1). Body elongate lanceolate .. .. *D. caudata* (*diegensis*)
Body not lanceolate 5
5 (4). Posterior sail present 6
No posterior sail 7
6 (5). Posterior sail ventral or antapical .. .. *D. hastata*
Posterior sail dorsal .. .. *D. uracantha*
7 (5). Plate extensions on posterior and dorsal margin; left sulcal list very wide at R_3 .. .. *D. tuberculata*
No plate-like extensions; left sulcal list moderate at R_3 8
8 (7). Ventral margin straight or slightly concave 9
Ventral margin sinuate 10
Ventral margin convex 11
9 (8). Body trapezoidal, base truncate, areoles very large .. .. *D. truncata*
Body quadrangular: base rounded with blunt angle at antapex, areoles moderate .. .. *D. schroederi*
Body suboval, base evenly rounded, areoles moderate .. .. *D. fortii*
10 (8). Body elongate, rather narrow .. .. *D. sacculus*
Body ovate .. .. *D. okamurai*
11 (8). Antapex acute, sculpture heavy .. .. *D. acuta*
Antapex rounded 12
12 (11). One to several protuberances on antapex, sculpture heavy .. *D. acuminata*
No protuberances on antapex 13
13 (12). R_3. Posterior main rib present 14
R_3. Absent or rudimentary .. .. *D. similis*
14 (13). Body broadly elliptical symmetrical 15
Body asymmetrical in lateral view .. .. *D. ovum*
15 (14). Body elliptical; anterior girdle list not ribbed .. .. *D. arctica*
Body oval; anterior girdle list ribbed .. .. *D. sphaerica*

Acuta group

DINOPHYSIS OVUM Schütt

Fig. 35*a-d*

Dinophysis ovum Schütt, 1895.
non *D. ovum* var. *baltica* Levander, 1900.

Body in lateral view somewhat irregularly oval, markedly asymmetrical. Apex narrower than the broadly rounded antapex, ventral contour to posterior main rib slightly convex, then more or less broadly and evenly rounded, dorsal contour always much more strongly convex than the ventral and continuous with antapical contour. Length 1.3-1.4 breadth. Widest at or just behind R_3. Midline on long axis or slightly behind dorsally and at 5-10°; anterior girdle list strong, thick-walled, a little broader than sulcus, set asymmetrically with apex, usually inclined dorsally, not ribbed (or ribbed, Schiller 1933). Kofoid and Skogsberg differentiated *D. sphaerica* from *D. ovum* by a ribbed anterior list in the former species, and a slightly different left sulcal list. Posterior list thick-walled and about $\frac{1}{2}$ as broad as the other. Left sulcal list 0.5-0.6 body length, outer edge almost straight or slightly convex. R_1 and R_2

of equal length, R_2 0.2-0.3 body length from R_3. Nucleus posterior, chromatophores yellow. Theca with thick poroids often with pores. 44-62 by 38-45 μ. The more northerly estuarine form is smaller and thinner-walled than the southern (antarctic) form.

Distribution.—Subtropical in Mediterranean, Adriatic, Atlantic, English Channel. Australia: Port Hacking, N.S.W.; Storm Bay, Tas.; Swan River, W.A.; Antarctic (B.A.N.Z.A.R.E.).

DINOPHYSIS SPHAERICA Stein emend Kofoid & Skogsberg

Fig. 36*a-c*

Dinophysis sphaerica Stein emend Kofoid & Skogsberg, 1928.

Body ovate to subellipsoidal in lateral outline, widest in or somewhat behind the middle. Length 1.17-1.43 breadth. Anterior girdle list 1.4-1.7 times wider than girdle, ribbed. Hypotheca symmetrical or almost so. Left sulcal list is *c.* 0.58 length of body, the 3 main ribs being of approximately equal length, not club-shaped. Differs from *D. ovum* in ribbed anterior girdle list and less-developed posterior portion of left sulcal list; from *D. similis* in having the main posterior rib of the left sulcal list well developed, and in the posterior portion of the list being angular instead of rounded. Whether *D. sphaerica* and *D. similis* are distinct from *D. ovum* is a matter of doubt. Probably *D. sphaerica* and *D. similis* are forms of *D. ovum.*

Distribution.—Widely distributed in all warm seas and also in cold water. Australia: Port Hacking, N.S.W.; Swan River, W.A.

DINOPHYSIS ARCTICA Mereschkowsky

Fig. 37*a, b*

Dinophysis arctica Mereschkowsky, 1879.
D. laevis (Bergh) Pouchet, 1883.
D. rotundata Levander, 1894.
D. granulata Cleve, 1899; Gran, 1902; Lemmermann, 1905.
?D. vanhöffenii Cleve, 1900.
non *D. laevis* Bergh, Claparède & Lachmann, 1899.
nec *D. rotundata* Claparède & Lachmann, 1899.

Body in lateral view more or less broadly elliptical, symmetrical, deepest in the middle, middle line identical with long axis. Length 1.2-1.4 breadth. Both girdle lists almost equally broad, or the anterior somewhat broader, as broad as or somewhat narrower than the girdle. Sulcal lists moderately developed, outer edge evenly convex. Yellow chromatophores. Theca with fine scattered or large closely distributed poroids. Sometimes at the antapical end is a small hemispherical bulge in the theca like that of *D. acuminata.*

Distribution.—In pack ice areas of Greenland and Spitzbergen, in open and coast water of the North Sea, Baltic, Barents Sea, and Atlantic. Not found in Australian waters but occurred in Heard I. plankton and in B.A.N.Z.A.R.E. Antarctic hauls.

DINOPHYSIS ACUMINATA Claparède & Lachmann

Fig. 38*a-c*

Dinophysis acuminata Claparède & Lachmann, 1859.
?Dinophysis vanhöffenii Ostenfeld, 1899; Cleve, 1900, 1914.
D. ellipsoides Kofoid, 1907.

Cell in lateral view elongated oval, symmetrical or only slightly asymmetrical when the dorsal contour is somewhat more strongly convex than the ventral. Epitheca low, apex more or less evenly convex. Straight or slightly hollowed. Antapex rounded or rather straight with several protuberances. Midline and long axis identical. Length 1.3-1.5 breadth. Both girdle lists smooth or spined, width of upper equal to girdle or somewhat broader. "Funnel" wide and low where the upper girdle list is more or less bent outwards. Left sulcal list small, not transparent, the 3 main ribs well developed, outer edge usually convex. Yellow chromatophores. Theca with numerous thick poroids. 38-51 by 22-38 μ.

A very variable form of which the boundaries are uncertain.

Distribution.—North Sea, Baltic, also in the east, almost fresh portion. English coast, common at Plymouth; in the southern part of the Bosphorus in the Mediterranean. Neritic, euryhaline, and eurythermic. Australia: Tasmania (rough theca with processes); Port Hacking, N.S.W.; Swan River, W.A.; South Australia ? (smoother theca).

DINOPHYSIS SIMILIS Kofoid & Skogsberg

Fig. 39

Dinophysis similis Kofoid & Skogsberg, 1928.
D. sphaerica Schütt, 1895 partim.
D. sphaerica Pavillard, 1916; Jörgensen, 1925.

Body subcircular to ovate or subellipsoidal in lateral outline, deepest at or just behind the middle, and 1.03-1.29 times longer than deep, symmetrical or slightly inclined posteroventrally. Anterior girdle list 1.42 times wider than girdle. Epitheca moderately convex; girdle flat or convex. Left sulcal list about ½ length of body, of uniform width, rounded posteriorly. Posterior main rib absent or rudimentary.

Distribution.—Probably widely distributed in tropical, subtropical, and warm-temperate seas. Australia: Port Hacking, N.S.W.

DINOPHYSIS OKAMURAI Kofoid & Skogsberg

Fig. 40

Dinophysis okamurai Kofoid & Skogsberg, 1928.
D. vanhöffeni Okamura, 1907 partim.

Body subovate in lateral outline, with dorsal shoulder-like constriction at girdle, and ventral margin somewhat concave between R_2 and epitheca, broadest in the middle, and 1.32-1.50 times longer than broad. Epitheca slightly convex, highest in the middle. Girdle flat or slightly concave, and about 3 times as high as epitheca. Anterior girdle list about as wide as girdle. Hypotheca somewhat asymmetrical, dorsal margin moderately convex, ventral margin somewhat concave in front of fission rib, behind this slightly convex or almost straight. Antapex uniformly convex, confluent with dorsal and ventral margins. Posterior portion of body wider than the anterior. Left sulcal list comparatively small, decreasing suddenly behind the posterior main rib.

Distribution.—Eastern Pacific. Japan, Australia: east coast, Montague I. to Port Hacking, N.S.W., quite common in Port Hacking, at times extending into brackish water at Audley. The estuarine forms resemble those of Okamura (1907) in size and shape, the neritic forms those of Kofoid and Skogsberg (1928). It seems to be endemic in Port Hacking, especially in the upper reaches.

DINOPHYSIS TRUNCATA Cleve
Fig. 41*a*, *b*

Dinophysis truncata Cleve, 1900.
D. cuneiformis Mangin, 1912; non Meunier, 1910.

Body in lateral view somewhat trapezoidal in outline. Epitheca raised from hypotheca. Dorsal and ventral margins diverging at a slight angle, antapex flatly arched, but sagittal margins rounded and confluent therewith. Epitheca very small. Girdle lists equal, ribbed, about as broad as the concave girdle, circumference of posterior girdle list wider than upper. Left sulcal list very long, as long as hypotheca; R_1 directed upward; R_2 clearly split; R_3 opposite the widest part of the body, directed backwards. The list ending in the flattened portion of the hypotheca. Theca sculptured with poroids regularly arranged. Length 60-70 μ, width at antapex 55-60 μ, at girdle 32-35 μ.

Distribution.—Southern cold area of Atlantic, Antarctic, Weddell Sea. Australia: Subantarctic; south-east coast of Tasmania, marine. In Storm Bay, Tas., as a guest.

DINOPHYSIS TUBERCULATA Mangin
Fig. 42*a*, *b*

Dinophysis tuberculata Mangin, 1919.
D. carinata Peters, 1928.

Body in lateral view variable, irregularly oval to almost pentagonal. Epitheca very low, length 1.2-1.4 breadth, greatest diameter at R_3. Epitheca flatly arched. Dorsal contour more or less convex, antapically broadly rounded or narrowly oval. Ventral contour to R_3 from the posterior girdle list is straight or slightly convex, then strongly curved to antapex. Anterior girdle list broader than girdle, higher posteriorly, ribbed or areolate. Posterior girdle list somewhat smaller than or as broad as anterior, sometimes ribbed. Left sulcal list broadly extended, more or less strongly sculptured and curved towards the right side of the body, about 2.3 body length, $\frac{1}{3}$-$\frac{2}{3}$ width of body. R_1 present or absent, also R_2 and R_3 well developed. Sagittal ridge narrow; with an antapical region, a border of plate-like projections which vary greatly in form; sculpture of the more or less thin theca strong and raised, areolate, with a poroid in each areole, sculpture extending to the lists; 68-82 by 50-59 μ.

Distribution.—Antarctic: Weddell Sea (B.A.N.Z.A.R.E.).

DINOPHYSIS ACUTA Ehrenberg

Fig. 43

Dinophysis acuta Ehrenberg, 1839.
D. ventricosa Claparède & Lachmann, 1859.
D. acuta var. *steinii* Lemmermann, 1902.

Body in lateral view more or less asymmetrical. Epitheca very flatly rounded, ventral and dorsal margins slightly diverging, broadest at R_3, and then with straight margins meeting in the conical antapex. Long axis making an angle with midline, length 1.5-1.6 breadth. Both girdle lists ribbed or reticulate, or not. Upper twice as broad as girdle. Left sulcal list strongly convex above. Near R_1 straight or more or less convex and almost evenly broad below, making varying angles with the conical central margin. Usually without, more rarely with sculpture, R_1 very strongly bent forward. R_2 concave, directed slightly upwards, R_3 more or less bent, directed backwards. Chromatophores yellow. Theca strongly sculptured, with large, mostly strongly marked poroids. Sculpture at times on the left girdle list (old forms).

Distribution.—Very widely distributed in European seas, Atlantic Ocean, and Arctic; Mediterranean. Euryhaline and eurythermic. Australia: south-west coast.

DINOPHYSIS SCHROEDERI Pavillard

Fig. 44

Dinophysis schroederi Pavillard, 1909.

Body elongated in lateral outline, deepest somewhat behind the middle, nearly twice as long as broad, dorsal margin moderately convex, ventral margin nearly straight in front of R_2, and more or less angular at R_3, narrowly rounded or subacute posteriorly. Longitudinal axis deflected posteroventrally. Markedly compressed in ventral view; margins parallel or slightly concave. Anterior girdle list nearly twice as wide as girdle, with or without ribs. Left sulcal list nearly $\frac{3}{4}$ body length. R_1 directed strongly forward, R_3 backward and curved posteriorly. End of list joins R_3 to angle of ventral margin.

Schiller records intergrades between *D. schroederi* and *D. acuta*.

Distribution.—Widely distributed in subtropical, warm-temperate, and temperate waters. Australia: east coast, Port Hacking, N.S.W.; Storm Bay, Tas.

DINOPHYSIS FORTII Pavillard

Fig. 45

Dinophysis fòrtii Pavillard, 1923.
D. laevis Bergh, Pouchet, 1883.

D. intermedia Pavillard, 1916.
D. intermedia forma *pachyderma* Jörgensen, 1923.

Body narrowly subovate in lateral view, with flattened ventral margin, and broadly, evenly rounded posteriorly, widest somewhat behind the middle, about 1½ times as long as wide. Markedly compressed in ventral view, margins almost parallel. Epitheca low, convex to flat, anterior girdle list twice as wide as girdle. May or may not be ribbed. Girdle usually flat. Left sulcal list more than ½ as long as body, wide, usually sculptured, posterior margin may be recurved. Hypotheca margin straight from R_1 to R_3, then evenly curved to dorsal margin, which is more or less evenly convex. Theca finely areolate.

Distribution.—Widely distributed in subtropical, warm-temperate, and temperate waters. Australia: east coast, Jervis Bay to Port Stephens, N.S.W.; Storm Bay, Tas.; south-west of Port Fairy, Vic.; Southern Ocean.

DINOPHYSIS SACCULUS Stein

Fig. 46

Dinophysis sacculus Stein, 1883 partim.
D. acuminata var. *reniformis* Pavillard, 1905.
D. pavillardi Schröder, 1906, 1911.
D. reniformis (Pavillard) Kofoid & Skogsberg, 1928.

Body in lateral view asymmetrical of varying form. Dorsal margin either undulating, convex below girdle, concave in the middle, and convex again towards the apex: without the concavity, or only a suggestion thereof, and then running straight to the antapical region; this is more or less convex or running obliquely ventrally to a blunt projection with several blunt projections below the ventral portion; or not humped but with the theca rough. From here the ventral contour is concave or slightly convex, and strongly convex from the end of the left sulcal list to the girdle. Length 1.2-2.3 breadth, greatest breadth occurs in different places in different specimens. Anterior girdle list somewhat broader than girdle. Left sulcal list reaching at least the middle of hypotheca, about 0.4-0.5 of body length; outer margin convex, ribs very marked. R_1 and R_2 curved, thorn-like, directed obliquely outwards. R_3 usually thicker than the other 2, little or no longer, thorn-like, curved backwards, end pointed or blunt, wing reaching little past R_3, making a sharp angle therewith. Theca with coarse structure. Poroids somewhat loosely arranged. 48-60 by 26-36 μ.

Distribution.—Mediterranean, Atlantic, Australia: Port Hacking, N.S.W.; Albany, W.A.; Storm Bay, Tas.

Hastata group

DINOPHYSIS HASTATA Stein

Fig. 47*a*, *b*

Dinophysis hastata Stein, 1883.
Phalacroma hastata Pavillard, 1909; Pavillard, 1916, 1923; Schiller, 1911, 1912; Schröder, 1911; Forti, 1922; Lebour, 1925.

Dinophysis hastata var. or forma *phalacromoides* Jörgensen, 1923.
D. hastata var. or forma *uracanthoides* Jörgensen, 1923.
D. uracantha var. *mediterranea* Jörgensen, 1923.
Phalacroma odiosum Pavillard, 1930.
D. hastata var. *parvula* Lindemann, 1923.

Body subovate, subobovate, or subellipsoidal in lateral outline; rounded subtruncate or truncate anteriorly; subacute or narrowly to broadly rounded posteriorly, deepest somewhat in front of to somewhat behind middle; length 1.1-1.6 breadth; longitudinal axis may be deflected posteroventrally. In dorsal view narrowly obovate, about 2.5 times longer than wide. Girdle sometimes but slightly inclined forwards; epitheca sometimes visible above anterior girdle list; the latter 1.5-2.5 times as wide as girdle; posterior list sometimes ribbed. Left sulcal list $\frac{1}{2}$-$\frac{3}{4}$ length of body, sometimes reticulate or with accessory ribs. R_3 inclined posteriorly, frequently long. Triangular to spine-like posterior sail at or ventral to midline, usually inclined ventrally and with or without central rib or reticulation, sometimes with marginal ribs. Separated from left sulcal list. Theca usually finely and closely areolate.

Distribution.—Widely distributed in tropical, subtropical, and warm-temperate seas, rare in colder waters. Australia: Port Hacking to Trial Bay, N.S.W.

DINOPHYSIS URACANTHA Stein

Fig. 48*a*, *b*

Dinophysis uracantha Stein, 1883.

Body subcircular to subovate in lateral view, seldom truncate anteriorly; deepest somewhat in front of to somewhat behind the middle; length 0.98-4 depth; longitudinal axis deflected posterodorsally at 0-13°. Anterior girdle list 1.5-2.5 times wider than girdle; epitheca seldom visible above this list. Left sulcal list 0.6-0.75 length of body; margin forms an angle of 20-40° at R_3, which is inclined posteriorly, sometimes with secondary ribs and reticulation with triangular or claw-like posterior sail located somewhat dorsally to midline, 0.4-0.9 greatest depth of body, with marginal but without central rib (specimen shows ventral rib separated from left sulcal list but otherwise agrees with Kofoid's description. Theca finely and closely areolate. Length 37.5-63.5 μ.

Distribution.—Widely distributed in tropical, subtropical, warm-temperate seas, seldom in colder waters. Australia: east coast, Trial Bay and Port Hacking, N.S.W.

Caudata group

It seems very doubtful whether the 3 species *Dinophysis diegensis*, *D. caudata*, and *D. tripos* are distinct species. In Walsh Bay in 1943 all forms encountered in the plankton were referred to *D. diegensis*, while in other parts of Sydney Harbour *D. caudata* was collected. In 1950-51, *D. caudata* was rare in Sydney Harbour, replaced by *D. diegensis*. In

Port Hacking, from 1940 to 1949, *D. tripos* predominated, with *D. caudata* as a minor plankton constituent. In 1950, *D. diegensis* was predominant with *D. tripos* rare. This suggests that *D. caudata* and *D. diegensis* are forms of the same species, and this is confirmed by the occurrence of intergrades between all 3. The close relationship of *D. tripos* and *D. caudata* was recognized by Bergh (1884). Lemmermann (1901, 1905), Ostenfeld and Schmidt (1901), Entz (1902, 1905), Schröder (1906), Lebour (1917), Paulsen (1908), and Okamura (1912) regarded *D. tripos* as a variety of *D. caudata*. Kofoid and Skogsberg (1928) considered that "the evidence seems to be in favour of the opinion of those who regard *D. tripos* as a distinct species". In the present investigation *D. tripos* predominated south from Sydney Harbour, and *D. caudata* has not been found in Tasmania. In and north of Sydney Harbour, e.g. Broken Bay, *D. caudata* predominated over *D. tripos*, which has not been found in tropical plankton tows. It is no doubt significant that Kofoid and Skogsberg did not record *D. tripos* in their material. This suggests that the latter is a cool-temperate form. The fact that they overlap without intergrades in areas of overlap suggests a specific difference. At any rate, the ecological significance of this makes it convenient to follow Kofoid and Skogsberg. *D. diegensis*, however, is regarded as a form of *D. caudata*. It has been found only in estuarine and neritic waters, and in this investigation only in the same areas as *D. caudata*.

DINOPHYSIS CAUDATA Saville-Kent

Fig. 49*a-e*

Dinophysis caudata Saville-Kent, 1881.

Synonymy.—The synonymy of this species is very complicated and readers are referred to the excellent discussion on the subject by Kofoid and Skogsberg (1928).

Body very variable in shape, elongated, deepest somewhat in front of to somewhat behind the middle, 1½-3¼ times as long as wide. Anterior portion irregularly obovate in lateral outline, subtruncate anteriorly; posterior portion more or less slender, pedunculate to tapering, transition between main and posterior portion gradual or more or less sudden, longitudinal axis inclined at 7-30°. In dorsal view strongly flattened, 7-8 times longer than wide. Anterior girdle list 1.5-2.5 times as wide as girdle. Left sulcal list extends to base of peduncle, margin forms an angle of 70°-110° at R_3 or this portion of list is recurved. R_3 about parallel to girdle; list more or less reticulate; theca finely and closely areolate. Length 71.8-110.0 μ.

Distribution.—Widely distributed in tropical, subtropical, and warm-temperate seas, seldom in colder waters. Australia: east coast, Port Hacking, N.S.W., to Moreton Bay, Queensland; New Guinea; Solomon Is.; west coast (Cape Inscription), south coast (Albany, W.A.) to west coast of Great Australian Bight.

Each area in Australia seems to have a characteristic form of *D. caudata* which is reasonably constant for that area, so that these forms have an ecological significance.

DINOPHYSIS CAUDATA var. DIEGENSIS (Kofoid)

Fig. 50*a-g*, including *caudata-diegensis* intermediates

D. diegensis Kofoid, 1907.
D. caudata var. *subdiegensis* Jörgensen, 1923.
D. kofoidi Jörgensen, 1923.

Body in lateral view elongated; epitheca low, flat, inclined ventrally; upper part of hypotheca with margins almost parallel to slightly diverging posteriorly, lower part conical, pointed posteriorly, and more or less affixed. In dorsal view the body is constricted, and has a more or less irregular margin. Right sulcal list narrow, reaching about R_2; left more or less broad, to below R_3, margin convex to straight. Midline and long axis almost identical, running through antapex or the latter inclined dorsally. Theca with scattered, very small poroids, 110 by 44 μ.

Distribution.—Pacific Ocean, Mediterranean, Australia: Sydney Harbour, Port Hacking, N.S.W.

DINOPHYSIS TRIPOS Gourret

Fig. 51*a-c*

Dinophysis tripos Gourret, 1883.
D. homunculus Stein, 1885 partim.
D. homunculus var. *tripos* (Gourr.) Lemmermann, 1900; Pavillard, 1905; Paulsen, 1908; Entz, 1902, 1905.
D. homunculus var. *appendiculata* Zacharias, 1906.

Body in lateral view elongate, unsymmetrical. Epitheca minute compared with hypotheca. Hypotheca ventrally almost straight or sigmoid to R_3, then margin concave to peduncle. The lower part of the body forms a long, bluntly conical process. Dorsal margin below girdle, slightly concave to straight, then convex, then a 2nd, pointed dorsal posteriorly directed or a blunt, often ventrally curved, process which often carries a small wing, uniting 2 daughter cells. Processes with knobs at bases only in forms occurring south of Bass Strait in oceanic water. Body in dorsal view strongly constricted. Anterior girdle list broad, forming a rather steep and high funnel, ribbed, and the margin either straight or with pointed teeth. Sulcal list unusually large, sometimes widely projecting at R_3 and often strongly sculptured. Theca with large poroids, often with a pore. Yellow chromatophores. 95-105 by 50-56 μ. Long axis inclined dorsally.

Distribution.—Warm-water form. Atlantic Ocean (Gulf Stream) to Norway and Greenland, perennial in Mediterranean. Australia, from Port Stephens, N.S.W., south to convergence, rare in more northerly waters, oceanic, neritic, and frequently estuarine; becomes papillate in southern regions.

DINOPHYSIS MILES Cleve

Fig. 52

Dinophysis miles Cleve, 1900.
D. miles forma *indica* Ostenfeld & Schmidt, 1901.
D. miles var. *aggregata* (Weber van Bosse) Lemmermann, 1901.
D. miles Cleve var. *maris rubri* Ostenfeld & Schmidt, 1901.
D. miles forma *maris jonii* Schröder, 1906.
D. aggregata Weber van Bosse, 1901.
Heteroceras schröteri Forti, 1901.

Body of very variable form. Epitheca very flat, sometimes hardly perceptible. Ventral margin of hypotheca to R_3 almost straight or strongly wavy, with a large bulge at R_3, from which the long antapical process begins. Dorsal contour from girdle convex, then running into a short or long extension which is concave ventrally, the concavity passing over suddenly or gradually into the dorsal process. This is either short, curved more or less from the base, straight, running obliquely backwards, and only the end part straight, or bent outwards and directed at right angles, carrying a wing which joins daughter cells; thickest at base, tapering gradually towards the end, and ending in a rounded, more or less broad, point, length 0.46-0.7 times the body length including the posterior process. Posterior process shorter or longer than, or as long as, the dorsal process; when shorter it is plump with a somewhat undulating contour, or longer and thinner, straight, seldom bent slightly ventrally, with a rounded or pointed end. Angle between antapical and dorsal processes 50°-90°. Body wider and shorter and plumper than both the processes and inverted. Anterior sulcal list broad or narrow, ribbed, with smooth or toothed edge, oblique to midline. Posterior girdle list similar. Left sulcal list runs to antapical process, often reaching the middle thereof. Right sulcal list of variable length, reaching R_3, narrower than the left. Theca with round or angular areoles each with a pore, or only with pores. Sometimes up to 8 daughter cells remain together. Length 125-150 μ.

Distribution.—Mediterranean, Red Sea, Indian Ocean, numerous at times near Java and Sumatra. Australia: north-west coast, Thursday I., northern New Guinea. Confined to tropical waters.

Genus AMPHISOLENIA Stein

Amphisolenia Stein, 1883.

Epitheca a small flat plate: hypotheca much drawn out longitudinally, consisting of head (with lists), neck, mid body, and antapical, all co-linear, but antapical may be sigmoid or branched.

KEY TO SPECIES OF THE GENUS AMPHISOLENIA DESCRIBED IN THIS PAPER

1.	Antapex with 2 branches	*A. thrinax*
	Antapical unbranched	2
2(1).	Antapical with "heel"	3
	Antapical without "heel"	4

3(2). Strong, short, pointed spinule on antapex . . . . *A. palmata*
Antapical truncate with 2 small spinules on antapex . . . . *A. bidentata*
4(2). Sigmoid curvature of body strong; minute spinule may occur in left valve . . . . *A. curvata*
Sigmoid curvature moderate: 2 stout lateral spinules, 1 on each valve *A. bispinosa*

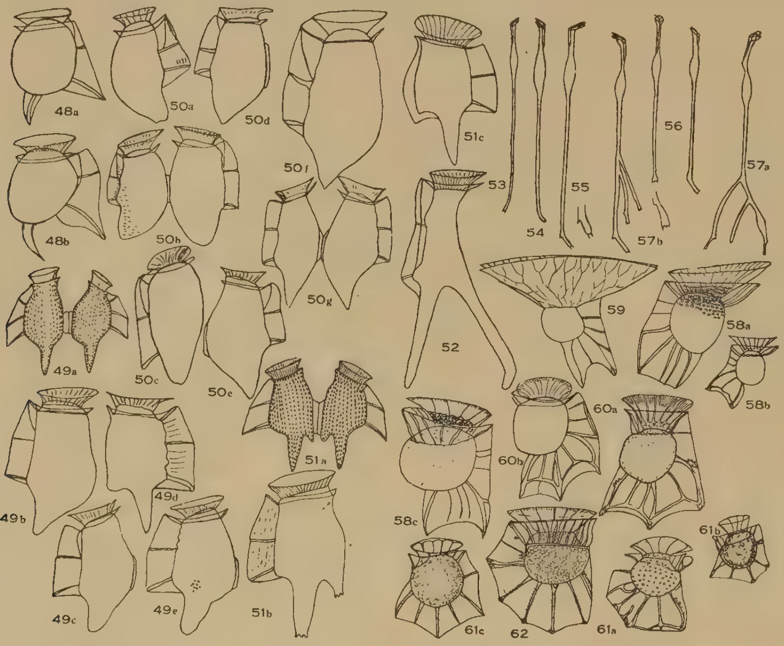

Fig. 48.—*a, Dinophysis uracantha* Stein, 1883. Trial Bay; *b, D. uracantha.* Jibbon Cape. Fig. 49.—*a, D. caudata* Saville-Kent, 1881. Port Jackson form; *b, D. caudata.* Walsh Bay form; *c, D. caudata.* Port Hacking (unusual form), 1940; *d, D. caudata.* Moreton Bay form; *e, D. caudata.* Buka Passage, Solomon Is., similar to the forms from north-west Australia. Fig. 50.—*a, D. caudata* var. *diegensis* (Kofoid). Port Hacking, 1940; *b, D. caudata* var. *diegensis.* Garden I. Port Jackson, 1951; *c, D. caudata* var. *diegensis.* Audley, Port Hacking, 1950; *d, D. caudata* var. *diegensis.* Garden I., Port Jackson, 1951; *e, D. caudata* var. *diegensis.* Walsh Bay, Port Jackson, 1942; *f, D. caudata* var. *diegensis.* Garden I., 1951; *g, D. caudata* var. *diegensis.* Garden I., 1951. Fig. 51.—*a, D. tripos* Gourret, 1883. Port Hacking; *b, D. tripos.* B.A.N.Z.A.R.E. St. 77, off S. Tasmania; *c, D. tripos.* Port Hacking. Fig. 52.—*D. miles* Cleve, 1900. New Guinea. Fig. 53.—*Amphisolenia bispinosa* Kofoid, 1907. Jibbon Cape. Fig. 54.—*A. curvata* Kofoid, 1907. Trial Bay. Fig. 55.—*A. bidentata* Schröder, 1900. Lord Howe I. Fig. 56.—*A. palmata* Stein, 1883. Off Trial Bay. Fig. 57.—*a, A. thrinax* Schütt, 1893. Lord Howe I.; *b, A. thrinax.* Trial Bay. Fig. 58.—*a, Ornithocercus heteroporus* Kofoid, 1907. Trial Bay; *b, O. heteroporus.* Jibbon Cape; *c, O. heteroporus.* Eden. Fig. 59.—*O. splendidus* Schütt, 1893. Port Stephens. Fig. 60.—*a, O. magnificus* Stein, sens. str. Schütt, 1895. Trial Bay; *b, O. magnificus*, Albany. Fig. 61.—*a, O. thurni* (Schmidt) Kofoid & Skogsberg, 1928. Trial Bay; *b, c, O. thurni,* Montague I. Fig. 62.—*O. steinii* Schütt, 1900. Trial Bay.

AMPHISOLENIA BISPINOSA Kofoid
Fig. 53

Amphisolenia bispinosa Kofoid, 1907.

With moderate sigmoid curvature. Head 2.2 times wider than long. Epitheca slightly convex. Mid body fusiform, passing imperceptibly into anterior process and antapical. Length 35-40 width. Antapical with gentle and even ventral concavity, posterior part very slightly inflated. Antapex rounded in lateral view with 2 stout, pointed, lateral spinules, 1 on each valve. Length 646-652 μ.

Distribution.—Tropical Pacific. Australia: rare on east Australian coast.

AMPHISOLENIA CURVATA Kofoid

Fig. 54

Amphisolenia curvata Kofoid, 1907.

With rather strong sigmoid curvature. Head 1.5 times wider than long. Epitheca flat or slightly convex. Mid body fusiform, merging gradually into anterior process, but rather well set off from antapical. Approximate distance from flagellar pore to antapical 4.7 length of neck. Length 12-13 width. Antapical with rather strong, even ventral concavity, approx. 4 times longer than neck; its posterior end very slightly widened. Antapex rounded, with a minute spinule on left valve (normally with 1 on each valve?). Length 463 μ.

Described by Kofoid from 1 specimen.

Distribution.—Tropical Pacific. Australia: coast of New South Wales, 1 specimen.

AMPHISOLENIA BIDENTATA Schröder

Fig. 55

Amphisolenia bidentata Schröder, 1900.

Slightly or moderately sigmoid. Head 2-3 times wider than long. Epitheca gently convex. Mid body fusiform, merging very gradually into anterior process and apical. Approximate distance from flagellar pore to antapical 3.5-5.5 times longer than neck. Length 30-67 width. Antapical approximately 8-13.5 times as long as neck, with gentle ventral concavity, its posterior part bent to the right 25-40° and twisted ventrally 90°, at point of bending left valve has a strong, short, pointed spinule which makes posterior part of antapical foot-like. Seen ventrally (torsion) antapex is widened, 2-3 times wider than average width of antapical, truncate, with 2 spinules one left valve, 1 on each corner, but none on right valve. Length 716-990 μ.

Distribution.—World-wide in tropical, subtropical, and warm-temperate waters. Australia: east coast, northern Tasman Sea, New Guinea, Coral Sea. Not found in estuaries (contrast *Phalacroma* and *Dinophysis*).

AMPHISOLENIA PALMATA Stein

Fig. 56

Amphisolenia palmata Stein, 1883.
A. bidentata Pavillard, 1916 partim.

Slightly or moderately sigmoid. Head 1.7-2.5 times as broad as long. Epitheca gently convex or flat. Mid body fusiform, merging very gradually into anterior process and antapical. Approximate distance from flagellar pore to antapical 3.3-5.0 times longer than neck. Length 27-42 width. Antapical 6.5-9.8 times length of neck, almost straight or with gentle ventral concavity; its posterior part bent to the right at 20-40° with or without ventral torsion of 90°. Posterior part of antapical as in *A. bidentata,* but right valve has strong, short, pointed spinule on antapex. Length 580-810 μ.

Distribution.—World-wide in tropical, subtropical, and warm-temperate regions. Australia: east coast. Rather rare.

AMPHISOLENIA THRINAX Schütt

Fig. 57*a, b*

Amphisolenia thrinax Schütt, 1893.

Resembling *A. bidentata,* but with 2 antapical branches. Length of antapical stem in front of 1st branch variable, 2.0-7.0 length of neck. Length 720-1049 μ. A variable species. Two specimens are depicted, 1 with 2 and 1 with 3 "feet".

Distribution.—World-wide in tropical, subtropical, and warm-water regions. Australia: east Australian coast, Lord Howe I.

Genus ORNITHOCERCUS Stein

Ornithocercus Stein, 1883.
Parelion Schmidt, 1888.
Ornithocerus Schütt, 1893.
Ornithoceras Gräf, 1909.

Body subcircular to obovate, compressed laterally: epitheca low, disk-like: girdle usually wide, especially dorsally, oblique; girdle lists large, anterior not stalked, posterior usually narrower than anterior; both with radial ribs and at times reticulations; no cross rib; right sulcal list small, left large, extending towards and often beyond antapex, often ribbed or reticulate. Type species *O. magnificus* Stein.

KEY TO SPECIES OF THE GENUS ORNITHOCERCUS DESCRIBED IN THIS PAPER

1.	Left sulcal list biangular	2
	Left sulcal list not biangular	5
2(1).	Left sulcal list ends at or near antapex	3
	Left sulcal list ends on dorsal side of body	*O. quadratus*
3(2).	Girdle lists much wider than body	*O. splendidus*
	Girdle lists less than body	4
4(3).	R_3 strongly clavate	*O. biclavatus*
	R_3 not clavate	*O. heteroporus*
5(1).	Left sulcal list with 3 lobes	6
	Left sulcal list with more than 3 lobes	*O. steinii*
6(5).	Left sulcal list with more than 8 radial ribs behind fission rib	*O. carolinae*
	Left sulcal list with less than 8 such ribs	7

7(6). Ribs c and e* of left sulcal list end at vertices at antapical and posteroventral lobes . . . . *O. thurni*
Ribs c and e of left sulcal list do not end at these vertices 8
8(7). Rib b biclavate, anastomosed with a rib . . . . *O. triclavatus*
Rib b not clavate . . . . *O. magnificus*

ORNITHOCERCUS HETEROPORUS Kofoid
Fig. 58*a-c*

Ornithocercus heteroporus Kofoid, 1907.

Lateral outline obliquely subellipsoidal or subcircular. Girdle lists 0.5-0.7, posterior 0.4-0.6 greatest depth of body; anterior with 5-7 radial ribs, the bases of which may be connected by reticulation; posterior with 9 or 10 usually simple ribs. Left sulcal list usually ends at or somewhat ventrally to antapex, but may extend somewhat further; with 2 lobes, 1 of which is posteroventral, the 2nd posterior; width at posteroventral lobe 0.56-1.06, at posterior lobe 0.54-1.06 the greatest depth of body; lobes narrowly rounded to subacute; large to fairly small, distance between tips 0.81-1.41 greatest depth of body, dorsal margin straight or gently convex to concave with 3-6 radial ribs and submarginal rib behind fission rib. Length 27.4-34.0 μ.

Distribution.—Widely distributed in tropical, subtropical, and warm-temperate seas. Rare in Mediterranean. Australia: east coast.

ORNITHOCERCUS SPLENDIDUS Schütt
Fig. 59

Ornithocercus splendidus Schütt, 1893.
O. splendens Schütt, 1896.
O. splendens Gräf, 1909.
Histioneis splendida Murray & Whitting, 1899.
Histioneis splendida Lemmermann, 1901.
H. splendidus Cleve, 1901, 1902.
Ornithocerus splendidus Theel, 1909.
O. magnificus Döflein, 1916.

Lateral outline subovate, subellipsoidal, subcircular, subtriangular, or subtrapezoidal. Girdle lists huge, anterior 0.8-1.5, posterior 0.8-1.4 greatest depth of body, both with 6-24 complete, sometimes irregular ribs with anastomoses. Left sulcal list ends at or somewhat ventrally to antapex, with 2 lobes, one posteroventral, the other posterior; width at posteroventral lobe 1-2, posterior 0.8-1.5 greatest depth of body; lobes narrowly rounded distally, sometimes long and narrow and sometimes small, distance between tips 0.8-2.0 greatest depth of body; dorsal margin straight, moderately convex, concave or sigmoid, with 2-5 often incomplete ribs behind fission rib; reticulations in lobes and often at tip of fission rib between lobes. Submarginal rib usually absent. Length of body 37-114 μ.

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* The ribs of the left sulcal list are lettered according to Kofoid and Skogsberg (1928) from the most dorsal rib (a) to R_3.

Distribution.—Widely distributed in tropical, subtropical, and warm-temperate seas. Australia: off Port Stephens, N.S.W.

ORNITHOCERCUS MAGNIFICUS Stein

Fig. 60*a*, *b*

Ornithocercus magnificus Stein, sens. str. Schütt, 1895.
non *O. magnificus* Bütschli, 1885; Chun, 1903; Whitelegge, 1891; Fricke, 1902; Willey & Hickson, 1909; Hjort, 1911; France, 1923.
Histioneis magnifica Murray & Whitting, 1899 partim; Entz, 1902, 1905; Pavillard, 1905 partim, 1916 partim; Meunier, 1910; Issel, 1921; Forti, 1922 partim?
H. magnificus Lemmermann, 1899, 1901 partim, 1905; Cleve, 1900 partim, 1901, 1902, 1903; Cleve, Ekman, & Pettersson, 1901, partim.
non *H. magnificus* Lemmermann, 1899 partim, nec. *H. magnifica* Schröder, 1900.
Ornithoceras magnificus Gräf, 1909.
Ornithocercus magnificus a Stüwe, 1909.
Ornithocercus minor Jörgensen, 1923.

Subcircular in lateral outline; girdle lists, anterior 0.5-0.9, posterior 0.5-0.7 greatest depth of body, anterior with 4-9 simple, complete, and some incomplete ribs. Left sulcal list ends on dorsal side of body at 0.3-0.6 greatest depth of body from posterior girdle list, with 3 narrowly rounded lobes, 1 posteroventral, 1 antapical, and 1 posterodorsal; that at posteroventral lobe 0.7-0.3, at antapical lobe 0.6-1.2, and at posterodorsal 0.7-0.2 greatest depth of body, typically with 5 ribs behind fission rib: distal ends of these ribs and fission rib connected by submerged rib; reticulation in each lobe; *a* rib extends into posterodorsal lobe; *b* and *c* ribs usually end dorsally to vertex of midlobe, *d* and *e* ribs dorsally to posteroventral lobe. Length of body 32-47 μ.

Distribution.—Widely distributed in tropical, subtropical, and warm-temperate seas. Australia: Eden, N.S.W., to Moreton Bay, Queensland, on east coast, not infrequent in Port Hacking; south of Albany, W.A.

ORNITHOCERCUS THURNI (Schmidt) Kofoid & Skogsberg

Fig. 61*a-c*

Ornithocercus thurni (Schmidt) Kofoid & Skogsberg, 1928.
?*Dinophysis galea* Pouchet, 1883 partim.
O. magnificus Stein, 1893 partim; Butschli, 1885; Whitelegge, 1891; Cleve, 1897 partim; Chun, 1903; Zacharias, 1906, 1907, 1911; Okamura, 1907 partim?; Willey & Hickson, 1909; Hjort, 1911; Faris & Cunha, 1917 partim; France, 1923.
Parelion thurni Schmidt, 1888.
Histioneis magnifica Murray & Whitting, 1899 partim; Lemmermann, 1899; Pavillard, 1906 partim.
Ornithocercus steinii Schütt, 1900, partim; Gran, 1912; Ostenfeld, 1915.
H. steinii Lemmermann, 1901 partim.
O. magnificus Fricke, 1902.
H. magnificus var. *steinii* Entz, 1902.
O. steinii Kofoid, 1907; Jörgensen, 1923.
O. magnificus var. *c* & *d* Stüwe, 1909.
H. magnifica var. *steinii* Forti, 1922.

Lateral outline subcircular. Girdle lists, anterior 0.5-0.8, posterior 0.5-0.75 times greatest depth of body, anterior with 5-9 complete ribs, often branched distally, and numerous short, marginal ribs; posterior with 11-16 complete and often simple ribs. Left sulcal list ends on dorsal side of body 0.1-0.4 the greatest depth of body from posterior girdle list, with 3 narrowly to fairly broadly rounded lobes, 1 of which is posteroventral, 1 antapical, and 1 posterodorsal; width at posteroventral lobe 0.6-1.2, at antapical 0.5-1.1, at posterodorsal 0.5-1.0 the greatest depth of body; typically with 5 ribs behind fission rib and with or without submarginal rib connecting these ribs; reticulation in each lobe; *a* rib extends into posterodorsal lobe, *b* rib ends ventrally to this lobe, and *c* and *e* ribs at vertices of antapical and posteroventral lobes. Length of body 43-81 μ.

Distribution.—Widely distributed in tropical, subtropical, and warm-temperate seas. Australia: Recorded from Green I., Sydney Harbour, N.S.W., by Whitelegge (1891); Maria I., Tas., to Moreton Bay, Queensland, on east coast.

ORNITHOCERCUS STEINII Schütt

Fig. 62

Ornithocercus steinii Schütt, 1900 sens. str.
O. magnificus Stein, 1883 partim.
O. steinii Schütt, 1900 partim.
O. serratus Kofoid, 1907; Kofoid & Michener, 1911; Faria & Cunha, 1917; Jorgensen, 1923.
O. magnificus var. *b* Stüwe, 1909.

Subcircular in lateral outline. Girdle lists, anterior 0.5-0.7, posterior 0.45-0.7 greatest depth of body. Anterior with 7-9 complete ribs, sometimes branched distally, and with some short marginal ribs; posterior with 10-19 complete and often simple ribs. Left sulcal list ends on dorsal side of body, at *a* near posterior girdle list, with 4 nearly equidistant, narrowly to fairly broadly rounded posterior lobes, viz. posteroventral, midventral, mid-dorsal, and posterodorsal lobes; width at posteroventral lobe 0.5-1.12, at midventral lobe 0.5-1.0, at mid-dorsal lobe 0.5-1.0, at posterodorsal lobe 0.5-1.0 greatest depth of body. Typically with 5 ribs behind fission rib and with reticulum in each lobe. Submarginal rib may be present; *a* rib ends near the middle of dorsal margin of list; each of *b* to *e* ribs ends at the vertex of 1 of the 4 lobes. Length of body 55-68 μ.

Distribution.—Widely distributed in tropical, subtropical, and warm-temperate seas. Australia: Trial Bay, N.S.W., to Moreton Bay, Queensland, on east coast. Appears at times in Port Hacking, N.S.W.

ORNITHOCERCUS QUADRATUS Schütt

Fig. 63*a-c*

Ornithocercus quadratus Schütt, 1900.
?*Dinophysis galea* Pouchet, 1883 partim.
Histioneis magnifica Schröder, 1900.

H. quadrata Lemmermann, 1901, 1904, 1905.
H. magnificus var. *quadratus* Entz, 1902, 1905.
O. magnificus var. *e* Stuwe, 1909.
H. magnifica var. *quadrata* Forti, 1922.
O. assimilis Jörgensen, 1923.

Lateral outline subcircular. Anterior girdle list 0.5-1.0, posterior 0.5-0.9 greatest depth of body; inclination of lists about the same as that of *O. steinii*. Left sulcal list ends in dorsal side of body at a distance from posterior girdle list about 0.5-0.65 greatest depth of body, either squarish or with 2 lobes, one posteroventral, the other posterodorsal in position. Width at posteroventral corner 0.6-1.1, at posterodorsal corner 0.5-0.9 greatest depth of body, with 3-8 ribs behind fission rib and usually with submarginal rib. Ribs very variable, sometimes with, sometimes without branches. Length of body 37-74 μ.

Distribution.—Widely distributed in tropical, subtropical, and warm-temperate seas. Australia: east coast, Montague I., N.S.W., to Moreton Bay, Queensland; off Black Diamond, and Port Fairy, Vic., west of Bass Strait; characterizes the eastern boundary of the west wind drift.

ORNITHOCERCUS CAROLINAE Kofoid

Fig. 64*a*, *b*

Ornithocercus carolinae Kofoid, 1907.

Almost circular in lateral view. Anterior and posterior girdle lists about ½ width of body, upper with 12-19 well-marked ribs, often with basal and distal anastomoses and a number of short marginal ribs, lower with 14-19 well-marked simple ribs, many of them can be joined by anastomoses. Left sulcal list ends on dorsal side of body, 0.4-0.7 times the greatest depth of body from lower girdle list, with 3 lobes, 1 posteroventral, 1 posterior, and 1 posterodorsal; the posterior lobe being the largest, and usually narrowly rounded, with 11-15 radial ribs, fission rib, and with reticulations on posterodorsal and posterior ribs. Submarginal rib can be present. 30.5-52 by 31.9-57 μ.

Distribution.—Widely distributed in tropical, subtropical, and warm-temperate seas. Australia: off Sydney, N.S.W., on 60-fm mark in 1951. Rare.

ORNITHOCERCUS TRICLAVATUS sp. nov.

Fig. 65*a*, *b*

A small, rather delicate species; body ovate with longitudinal axis at about 60° to girdle plane. Anterior girdle list flaring, about ½ depth of body, ribbed, posterior list slightly narrower, ribbed. Right sulcal list wide, trapezoidal with 3 or 4 ribs behind fission rib, ending somewhat dorsally to anterior, with 2 lobes, 1 with marginal rib joined to body by 2 plane ribs. Rib *a* ends in clavate extension of *b* rib, which has 2 large clavate swellings at right angles to each other, the dorsal swelling forming a marginal rib to the dorsal lobe. Theca porulate, resembles *O. heteroporus* and *O. geniculatus* Dangeard, 1927.

Only 1 specimen seen. Body 20 μ; total dimensions 50 by 60 μ.

Distribution.—East Australia, north of Sydney.

ORNITHOCERCUS BICLAVATUS sp. nov.

Fig. 66

A small species, rather similar in appearance to *O. triclavatus,* and obviously related to *O. heteroporus.* Body ovate, longitudinal axis at an angle of about 75° to girdle plane. Anterior girdle list ribbed, posterior not ribbed. Left sulcal list concave to R_3 with a ventral lobe without marginal rib. Rib *a* and R_3 swollen, rugose, with 3 fine ribs between them. Theca porulate, 25 μ. Overall size 45 by 50 μ.

Distribution.—East Australia, north of Sydney.

Genus PARAHISTIONEIS Kofoid & Skogsberg

Parahistioneis Kofoid & Skogsberg, 1928.

Body subrotund, subovate, rounded squarish, carafe-like, or gourd-like in lateral outline, usually slightly longer than deep. Epitheca small, nearly flat to rather strongly vaulted. Girdle wide, usually wider dorsally than ventrally; lists large, anterior funnel-shaped, usually not stalked, with 1-14 radial ribs; posterior usually forms a closed, cylindrical, upright collar with less than 6 radial ribs and without a submarginal cross rib. Right sulcal list small, ventral margin usually attached to left (except in *P. rotundata*). Left sulcal list usually large, with but 1 posterior lobe and 1 complete radial rib behind fission rib.

KEY TO SPECIES OF THE GENUS PARAHISTIONEIS DESCRIBED IN THIS PAPER

Anterior girdle list sessile	*P. rotundata*
Anterior girdle list stalked	*P. reticulata*

PARAHISTIONEIS ROTUNDATA (Kofoid & Michener) Kofoid & Skogsberg

Fig. 67

Parahistioneis rotundata (Kofoid & Michener) Kofoid & Skogsberg, 1928.
Histioneis rotundata Kofoid & Michener, 1911.

Body subcircular in lateral outline; length 13 depth; dorsally the girdle is gently concave, 0.48 depth of body, 1.3 times wider than ventrally, and inclined posterodorsally at 20°. Distance from apex to posterior girdle list 0.23 length of body. Anterior girdle list with short stalk, flaring distally with straight sides to an asymmetrical funnel 1.5 wider dorsally than ventrally. Height 0.64 depth of body. Posterior girdle list appears to be open ventrally; with 5 or 6 simple complete ribs, dorsal height 0.39 depth of body. Left sulcal list ends somewhat ventrally to antapex, narrowly rounded at R_3; margin rather strongly convex just behind R_2, dorsal margin gently concave. R_2 0.32 depth of body. R_3 submarginal, of moderate strength, 0.78 depth of body; from near the middle of R_2 a rib runs posteriorly, subparallel to margin of list; between R_2 and R_3 are 4 incomplete ribs.

Distribution.—Tropical Pacific.

The single specimen was found in plankton from Trial Bay, N.S.W., It does not agree completely with Kofoid and Skogsberg's description, but it seems futile to create a new species on 1 or a few specimens in what appears to be an exceedingly variable group. Both *Parahistioneis* and *Histioneis* show a number of "species" described by a single author and specimens are so rare that it seems impossible to consider the range of variability or the taxonomic criteria.

PARAHISTIONEIS RETICULATA (Kofoid) Kofoid & Skogsberg
Fig. 68

Parahistioneis reticulata (Kofoid) Kofoid & Skogsberg, 1928.
Histioneis reticulata Kofoid, 1907; Okamura, 1912.

Body gourd-shaped in lateral outline, with long, oblique anterior process; hypotheca semicircular; length 1.15-1.35 depth. Dorsally girdle is very strongly concave, 0.48-0.54 depth of body, 1.5 as wide as ventrally and inclined posterodorsally at 50°. Distance from apex to posterior girdle list 0.5 length of body. Anterior girdle list sessile, its height 0.3-0.4 depth of body. Posterior girdle list closed, a large part of it finely reticulated; dorsal height 0.34-0.43 height of body. Left sulcal list narrow, ends at or somewhat ventrally to antapex. Strikingly sigmoid between R_2 and R_3; R_2 0.12 depth of body. R_3 arises 0.09-0.20 depth of body from dorsal end of list, strong but not club-shaped, 0.27-0.37 depth of body. Reticulated. Length 35.9-44.0 μ.

Distribution.—Tropical and subtropical Pacific; Australia: Trial Bay, N.S.W.

Genus HISTIONEIS Stein

Histioneis Stein, 1883.

Body of diverse shapes, usually deeper than long: epitheca low, disk-like; girdle wide, widening dorsally, lists large, closed; anterior funnel-like and stalked; posterior usually subcylindrical and always with 1 dorsal and 1 ventral pair of ribs and 1 cross rib. Left sulcal list usually large, of diverse shapes, usually tongue-shaped, never with more than 1 main rib behind fission rib.

Type species. *H. remora* Stein des. Kofoid & Skogsberg.

KEY TO SPECIES OF THE GENUS HISTIONEIS DESCRIBED IN THIS PAPER

1.	Body kidney-shaped	2
	Body slipper-shaped	3
2(1).	Wing sculpture behind fission rib reticulate	*H. hippoperoides*
	Wing sculpture behind fission rib concentric	*H. dolon*
3(1).	Wing tongue-shaped; entire	*H. carinata*
	Wing tapering posteriorly to a point; perforated	*H. depressa*

HISTIONEIS DEPRESSA Schiller

Fig. 69

Histioneis depressa Schiller, 1928.

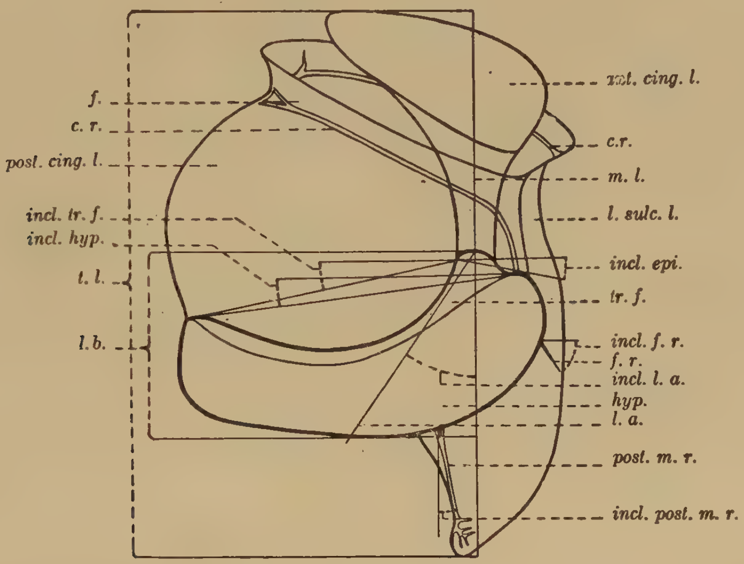

Fig. *C.*—Terminology and methods of measurement in *Histioneis.* Terminology.—The midline is the line drawn through the centre of the epitheca and the central axis of the proximal portion of the anterior cingular list. If longitudinal axis of the body were not inclined, it would coincide with the midline. In the specimen represented the longitudinal axis of body is inclined *posterodorsally,* the transverse furrow *dorsoposteriorly,* and the epitheca *ventroposteriorly.* The fission rib (R_2) is the rib of left sulcal list at place where this list is divided in binary fission. The posterior main rib (R_3) is the rib of left sulcal list near posterior end of this list, or, if more than one rib is present in this region, the best developed of these. The frill is the portion of posterior cingular list in front of cross rib, i.e., the rib that in the more or less primitive species runs about parallel to anterior margin of this list (after Kofoid and Skogsberg).

Body in lateral view somewhat kidney-shaped, dorsally prominent, strongly convex; epitheca low, flat, apex slightly concave; length 0.53 depth. Dorsal length of girdle 0.44 depth of body, almost 4 times as long as ventral. Apex only minute. On it sits the upper girdle list, which is tubular to above the middle, then rapidly becoming funnel-shaped; funnel flat dorsally, ventrally steep with thorn-like, branching ribs. Lower girdle list about as high dorsally as ventrally, 0.53 depth of body, usually with 2 transverse ribs of which the lower has 6-8 short ribs pointed above and reaching the upper. Left sulcal list narrow, pointed below, strongly sculptured. Only the lower R_2 clearly marked, strong, bow-shaped, joining R_3. This runs from about the middle of the antapex at right angles backwards to the point of the list. The window formed by R_2 and R_3 and the antapical wall apparently or actually perforated. Total length 60-65 μ; width 26-27 μ.

Distribution.—Adriatic. Australia: Trial Bay, N.S.W.

HISTIONEIS HIPPOPEROIDES Kofoid & Michener

Fig. 70

Histioneis hippoperoides Kofoid & Michener, 1911.

Body short, saddle-shaped, higher dorsally than ventrally; length 0.77 depth. Dorsally girdle is 0.37 depth of body, 5-6 times wider than ventrally, inclined anterodorsally 5-10°, and moderately concave. Distance from apex to posterior girdle list about 0.2 the base of this list. Anterior girdle list with a long stalk; its height 1.03 depth of body, 2.0-2.5 times wider distally than proximally, flaring but little and only in the distal ⅓. Dorsal height of posterior girdle list 0.9 depth of body; frill wide, with secondary frill 0.15-0.17 as high as list, having 12-17 simple ribs. Left sulcal list rather large, tongue-shaped, with large rounded, posterodorsal transverse fin 1.0 depth of body; R_2 almost straight, deflected posteriorly at about 35°; R_3 located midway between R_2 and antapex, with a few perpendicular ventral branches. Length of list 1.12 depth of body. Theca with pores only. Total length 95 μ.

Distribution.—Eastern tropical; Pacific; Australia: Montague I., N.S.W. (lat. 36°S.).

HISTIONEIS CARINATA Kofoid

Fig. 71

Histioneis carinata Kofoid, 1907.
?*Histioneis paulseni*, Okamura, 1912.
?*Histioneis remora* Jörgensen, 1923.

Body short, boat-shaped. Ventrally markedly higher than dorsally. Length 0.6 width, girdle dorsally 0.5 width of body, 5 times broader than ventrally, inclined 15-20° posterodorsally, gently concave. Apex rises from posterior girdle list, 0.11 the base of this list. Anterior girdle list with stem about ¼ total height, and including an angle of 70°. Height about 0.6 width of body. Lower girdle list with faint ventral reticulation: dorsal height 0.6 width of body. Left sulcal list with well-developed reticulation; R_2 straight, 0.18 width of body, bent posteriorly 25-30°, margined, strong, reticulate below, 0.63 breadth of body, lying in the midline, directed posteriorly, ventral border sigmoid, markedly convex below, narrowly rounded or angular. Theca reticulate. Total length 88 μ. Body length 31.4 μ, width 50 μ.

Distribution.—Eastern tropical Pacific, Japan ?; Mediterranean ?; Australia: east coast (Port Macquarie, N.S.W.).

HISTIONEIS DOLON Murray & Whitting

Fig. 72*a*, *b*

Histioneis dolon Murray & Whitting, 1899.

Body small, saddle-shaped, dorsally higher than ventrally. Length 0.7 width. Girdle 0.5 width of body dorsally, 10-15 times broader than ventrally, inclined 1-10° anterodorsally, strongly concave. Distance of

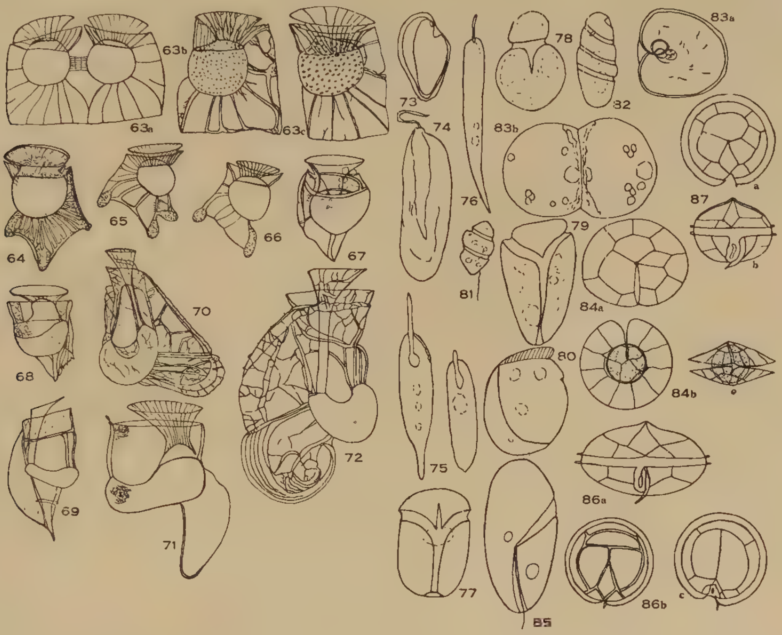

Fig. 63.—*a*, *Ornithocercus quadratus* Schütt, 1900. Cape Byron, *b*, *O. quadratus*, Trial Bay; *c*, *O. quadratus*. Montague I. Fig. 64.—*a*, *O. carolinae* Kofoid, 1907. Off Sydney; *b*, *O. carolinae*. Off Sydney. Fig. 65.—*a*, *O. triclavatus* sp. nov. Trial Bay; *b*, *O. triclavatus* sp. nov. Trial Bay. Fig. 66.—*O. biclavatus* sp. nov. Trial Bay. Fig. 67.—*Parahistioneis rotundata* (Kofoid & Michener) Kofoid & Skogsberg, 1928. Trial Bay. Fig. 68.—*P. reticulata* (Kofoid) Kofoid & Skogsberg, 1928. Trial Bay. Fig. 69.—*Histioneis depressa* Schiller, 1928. Trial Bay. Fig. 70.—*H. hippoperoides* Kofoid & Michener, 1911. Montague I. Fig. 71.—*H. carinata* Kofoid, 1907. Port Macquarie. Fig. 72.—*a*, *b*, *H. dolon* Murray & Whitting, 1899. Port Macquarie. Fig. 73.—*Oxyrrhis marina* Dujardin, 1841. Port Hacking. Fig. 74.—*Pronoctiluca pelagica* Fabre-Domergue, 1889. East Australia. Fig. 75.—*P. spinifera* (Lohmann) Schiller, 1937. Sydney Harbour. Fig. 76.—*P. acuta* (Lohmann) Schiller, 1933. Sydney Harbour. Fig. 77.—*Amphidinium inflatum* Kofoid, 1911. Garden I., Sydney Harbour. Fig. 78.—*A. kesslitzi* Schiller, 1928. Garden I., Sydney Harbour. Fig. 79.—*A. klebsi* Kofoid & Swezy, 1921. Port Hacking. Fig. 80.—*A. sulcatum* Kofoid, 1907. Port Hacking. Fig. 81.—*Cochlodinium helix* (Pouchet) Lemmermann, 1889. Port Hacking. Fig. 82.—*C. archimedes* (Pouchet) Lemmermann, 1899. Fig. 83.— *a*, *Noctiluca miliaris* Suriray (Lamarck, 1816). Garden I.; *b*, *N. miliaris*. Garden I. Dividing or conjugating forms? Fig. 84.—*a*, *Pyrophacus horologicum* Stein, 1883; *b*, *e*, *P. horologicum* var. *steinii* Schiller, 1937. Fig. 85.—*Hemidinium nasutum* Stein, 1883. Port Hacking. Fig. 86.—*Diplopsalis lenticula* Bergh, 1882, *a*, Ventral view; *b*, epitheca; *c*, hypotheca. Port Hacking. Fig. 87.—*D. lenticula* forma *minor* Paulsen, 1907. *a*, Epitheca; *b*, ventral view, Port Hacking.

apex from posterior girdle list 0.8-0.1 the base of this list. Anterior girdle list with a long stem, height 1.7-2 width of body, distally 10-12 times broader than proximally. Posterior girdle list with lateral pouches. Dorsal height of this list 1.4 width of body, collar wide with secondary collar 0.2-0.3 height of list, showing 6 or 7 simple ribs (not simple in specimen in Fig. 72). Left sulcal list large, tongue-shaped, with large, round posterodorsally directed transverse margin, 1.5-1.64 width of body. R_2 almost straight, inclined posteriorly about 35°. R_3 lying in the middle between R_2 and antapex, almost unbranched. Length of list 1.7-1.9 width of body. Theca only with pores. Total length 139-156 μ. Body 28.9 μ, width 37.1 μ

Distribution.—Widely distributed in tropical and subtropical seas. Australia: east coast, Port Macquarie, N.S.W.

Family **PRONOCTILUCIDAE** Lebour

Genus OXYRRHIS Dujardin

Oxyrrhis Dujardin, 1841.
Glyphodinium Fresenius, 1865; Cohn, 1866.

Body somewhat oval, asymmetrically contracted posteriorly to the left; girdle post-median, incomplete dorsally, and lacking a posterior margin. Sulcus spreading ventrally and posteriorly divided in front by the tentacular lobe. Transverse flagellum not ribbon-like but simple, springs from left of this lobe, longitudinal flagellum from right. Nucleus with beaded chromatin. Marine. Reproduction by oblique fission. Type species *O. marina* Dujardin. Monospecific genus.

OXYRRHIS MARINA Dujardin

Fig. 73

Oxyrrhis marina Dujardin, 1841.
Glyphodinium marinum Fresenius, 1865; Cohn, 1866.

Species description as for genus.

Distribution.—Marine and brackish water, cosmopolitan. Australia: Port Hacking, N.S.W.

Genus PRONOCTILUCA Fabre-Domergue

Pronoctiluca Fabre-Domergue, 1889.

Cell with ventral anterior tentacle and sulcus; anterior girdle feebly developed. Long, thread-like transverse flagellum, short or long longitudinal flagellum. Type species *P. pelagica* Fabre-Domergue.

Pelagorhynchus Pavillard, 1917.
Rhynchomonas Lohmann, 1902.

PRONOCTILUCA PELAGICA Fabre-Domergue

Fig. 74

Pronoctiluca pelagica Fabre-Domergue, 1889.
Rhynchomonas marina Lohmann, 1902; 1909, 1912, 1920; Lüke, 1913; Ostenfeld & Paulsen, 1904; Gran, 1915.

Pelagorhynchus marinus Pavillard, 1917.
Protodinifer marinum (Lohm) Kofoid & Swezy, 1921.

Cell spindle-shaped or pear-shaped, length about 2½ transdiameters. Tentacle slender, terminal. Girdle and sulcus anterior. Both flagella long, one anterior, the other posterior. Punctuated membrane covering cell. Nucleus with large bead-like chromatin granules; large yellow mass posteriorly. Encystment occurs in a thin closely adherent membrane from which a tentacle protrudes. Later the cyst expands into a sphere, and the body assumes a pear shape within it. Length 12-15 μ.

Distribution.—Marine. Mediterranean; Atlantic Ocean; North and South Baltic. Probably cosmopolitan. Australia: south-east coast.

PRONOCTILUCA SPINIFERA (Lohmann) Schiller

Fig. 75

Pronoctiluca spinifera (Lohmann) Schiller, 1937.
Pronoctiluca tentacula (Kofoid & Swezy) Fabre-Domergue, 1889.
Rhynchomonas spinifer Lohmann, 1920.
Protodinifer tentaculum Kofoid & Swezy, 1921.
Protonoctiluca pelagica Fabre-Domergue, Kofoid, 1931.

Body narrow, elongated, slightly asymmetrical, broadest in the posterior ⅓. Length 2-2.5 diameters. Apex asymmetrical, blunt-hemispherical, with almost straight, parallel walls or broadening to near the antapex, usually ending in a short blunt process. Girdle and sulcus and flagellar pores as in *P. pelagica*. Tentacle process slender, cylindrical, length about ½ a diameter, moving idly, often bent sideways.

Distribution.—Mediterranean; Atlantic and Pacific Oceans. Australia: east coast, Trial Bay, Port Hacking, Sydney Harbour, N.S.W.

PRONOCTILUCA ACUTA (Lohmann) Schiller

Fig. 76

Pronoctiluca acuta (Lohmann) Schiller, 1933.
Rhynchomonas acuta Lohmann, 1912.

Body pronouncedly spindle-shaped, slender, broadest in the 1st ⅓. Length 3-4 diameters, apex broadly rounded. Body tapering regularly to a conical point. Tentacle about ¼ body length.

Distribution.—Cool water of the Atlantic.

PRONOCTILUCA ACUTA var. CURVATA (Lohmann) Schiller

Fig. 75

Pronoctiluca acuta var. *curvata* (Lohmann) Schiller, 1933.

Anterior end of body as in type, posterior end very long, ending in a sharp, bent point. Flagella unknown. Length 60 μ.

Distribution.—In the southernmost Falkland stream. Australia: Sydney Harbour, N.S.W.

Genus AMPHIDINIUM Claparède & Lachmann

Amphidinium Claparède & Lachmann, 1899.

Body usually compressed dorsoventrally and sometimes laterally but may be round in sections: girdle far anterior with little or no displacement; sulcus extending either from girdle to hypocone or invading epicone, usually not twisted: epicone relatively minute, usually asymmetrical. Pusules may be present. Plasma colourless with or without chromatophores or coloured without chromatophores. Surface smooth or with fine striae, furrows, or ridges. Outer pellicle may be thick. Cysts may occur. Nutrition chiefly holophytic, may be holozoic. Type species *A. operculatum* Clap. & Lach.

AMPHIDINIUM INFLATUM Kofoid

Fig. 77

Amphidinium inflatum Kofoid, 1911.

Cell body broadly elliptical, saccate, ventrally contracted; in transverse view slightly flattened ventrally, length 1.52 diameter. Epitheca dome-shaped, apex rounded. Hypotheca saccate, almost cylindrical in the upper portion, antapex broadly rounded. Ventral region constricted in the middle; girdle in upper ⅓ of body, forming a broad V on the ventral side, dorsally horizontal, deeply depressed, with sharp, overhanging margins. Sulcus stretches from near apex, narrow, and widens only slightly near the girdle, tapering again towards the antapex. The upper flagellar pore lies at the junction of the proximal ends of the girdle and sulcus. Theca not striate, clearly double-contoured. Cell contents consist of an oval, rather large nucleus lying transversely, surrounded by elliptical plate-like yellow chromatophores, small oil deposits lying near the nucleus, and a spherical blue-green amyloplast.

Distribution.—Japan; Sydney Harbour, N.S.W.

AMPHIDINIUM KESSLITZI Schiller

Fig. 78

Amphidinium kesslitzi Schiller, 1928.

Epitheca head-shaped, more than hemispherical. Hypotheca elongate ovate, broadest in the middle, not contracted. Girdle low, deep, circular: sulcus beginning at girdle, with a very long longitudinal and a shorter transverse flagellum. Cell contains at most 5 pale green, irregularly arranged, plate-like chromatophores. 7-8 by 5-6 μ.

AMPHIDINIUM KLEBSI Kofoid & Swezy

Fig. 79

Amphidinium klebsi Kofoid & Swezy, 1921.
Amphidinium operculatum Klebs, 1884; Paulsen, 1908.

Cell oval, rounded posteriorly, girdle running down the hypocone for nearly ½ its length, sulcus extending from girdle oblique to the right, ending on right side. Epicone tongue-shaped, deflected to the left. Flagellar pores close together near the junction of girdle and sulcus. Nucleus large, oval, posterior. Yellow chromatophores radiating from a central mass sometimes behind the centre. Surface of cell faintly striate. At the anterior part of the epicone is an orange spot. Holophytic.

Distribution.—Port Erin (Isle of Man), Cullercoats (England); Gulf of Naples; Adriatic; Australia: Port Hacking, N.S.W.

AMPHIDINIUM SULCATUM Kofoid

Fig. 80

Amphidinium sulcatum Kofoid, 1907.

Body compressed oval, broadly oval in lateral view, ellipsoidal in ventral view, widest about midway between girdle and antapex. Epitheca low, highest laterally and dorsally and hollowed out towards sulcus, which passes dorsally beyond apex. Hypotheca broadly rounded posteriorly and very deeply channelled ventrally by sulcus, which deepens as it passes posteriorly from ventral pore. Right lip higher than left. Girdle anterior and sulcus very deep, oblique posteriorly, narrows distally to a slender channel displaced posteriorly the width of the proximal end of the furrow. Flagellar pore lies to the left of tongue of epitheca, extended posteriorly between longitudinal pores. Nucleus sphaeroidal, in the middle of hypotheca, with moniliform chromatin reticulum and 2 polar centrosomes sunk into its substance. A pyriform vacuole lies near the flagellar pore, and small, angular, yellowish chromatophores are scattered about the amyloid body. Plasma dense and coarsely granular. Length 68 μ, diameter 35 μ, thickness 54 μ.

Distribution.—Pacific Ocean, California. Australia: Port Hacking, N.S.W.

Genus COCHLODINIUM Schütt

Cochlodinium Schütt, 1896.

Gymnodiniidae with twist of body of at least 1.5 turns. Girdle a descending left spiral of 1.5 or more turns, widely displaced. Sulcus with or without apical and antapical loops, and with a twist of 0.5 or more turns. Nucleus usually central or posterior. Pusules usually present, opening into flagellar pore, often united; no nematocysts: plasma colourless to highly coloured. Usually holozoic. Type species *C. geminatum* (Schütt) Schütt.

COCHLODINIUM HELIX (Pouchet) Lemmermann

Fig. 81

Cochlodinium helix Lemmermann, 1889.
Gymnodinium helix Pouchet, 1887; Paulsen, 1908, Schütt, 1895.
non *C. helix* Kofoid & Swezy, 1922.

Cell distinctly coiled, outline oval, with both girdle and sulcus deeply impressed. Transverse section round. Epicone round to subconical. Girdle beginning far anteriorly and making 2 turns, the last part running round a posterior process which looks like part of the coil uncurled. Girdle displaced about 1 transdiameter. Sulcus narrower than girdle, invading epicone in a slight curve, and joining the girdle where anterior flagellar pore is situated, then sweeping round, making 1 complete turn from its anterior junction with the girdle and joining the girdle posteriorly, runs straight down to antapex. Posterior flagellar pore at posterior junction of girdle and sulcus. Nucleus central. Colour yellow, diffuse or in masses. Flagella rarely seen, both short. Sometimes contained in a thin-walled case, tight or loose. Length 32-45 μ.

Distribution.—English coast; Atlantic Ocean. Australia: Port Hacking, N.S.W.

COCHLODINIUM ARCHIMEDES (Pouchet) Lemmermann

Fig. 82

Cochlodinium archimedes (Pouchet) Lemmermann, 1899.
Gymnodinium archimedes Pouchet, 1883.

Body ellipsoidal, asymmetrical: length 2.05 transdiameter. Girdle a descending spiral of 2.5 turns, deeply impressed. Sulcus following course of girdle for 1.5 turns, shallow. Nucleus anterior. Near centre of body is a sphere formed by short rodlets, radially arranged. Anteriorly is a large, red pigment mass, possibly food remains. Length 75 μ.

Distribution.—Brittany coast; Australia: Port Hacking, N.S.W.

Family **NOCTILUCIDAE** Saville-Kent

Genus NOCTILUCA Suriray

Noctiluca Suriray, 1836 (mss. Lamarck, 1816).

Body inflated, somewhat reniform to spheroidal. Distinction between epicone and hypocone obliterated in the adult by the loss of girdle resulting from the formation of large vacuoles. Sulcus very deep, the mouth region extended anteriorly in the depression known as the apical trough. Girdle probably represented only by a small ventral portion. Longitudinal flagellum short, transverse flagellum reduced to a projecting mobile membrane or tooth. Tentacle at posterior end of sulcus. Plasma much vacuolated, the strands of protoplasm running from periphery to the central mass containing nucleus. Colourless to bluish green, sometimes tinged with yellow in centre. Multiple fission produces zoospores with girdle, 1 flagellum, and tentacle. Diameter 200-2000 μ.

NOCTILUCA MILIARIS Suriray

Fig. 83*a*, *b*

Noctiluca miliaris Suriray, 1836 (mss. Lamarck, 1816).
Medusa marina Slabber, 1771.
Medusa scintillans Macartney, 1810.
Slabberina Oken, 1815.
Noctiluca scintillans (Macartney) Kofoid & Swezy, 1921; Lebour, 1925.

Memmaria scintillans Ehrenberg, 1834.
Noctiluca marina Ehrenberg, 1834.
N. banksii var. Ehrenberg, 1834.
N. punctata Busch, 1851.
N. omogenea Giglioli, 1870.
N. pacifica Giglioli, 1891.

Monospecific genus. Species with characters of genus.

Distribution.—Neritic, marine, cosmopolitan. Australia: east coast estuaries.

Family **GLENODINIIDAE** Lebour

Genus PYROPHACUS Stein

Pyrophacus Stein, 1883.

Cell low, biconvex, lens-shaped; epitheca and hypotheca equal; plate formula 5-7′0 *a* 9-12″, 9-12‴, 3-4⁗. A marine form with hard shell; a few small plates in the sulcal region; autotrophic; reproduction by 2-4 spores. Type species *P. horologicum* Stein.

PYROPHACUS HOROLOGICUM Stein

Fig. 84*a*

Pyrophacus horologicum Stein, 1883.

Cell low, biconvex, lens-shaped, epitheca and hypotheca equal. Plate formula 5′ 9″ 9‴ 3⁗. Longitudinal furrow shows a few small plates. Autotrophic. Reproduction by 2-4 spores.

Distribution.—Northern Atlantic Ocean; North Sea; Baltic. Very numerous on the coast of Britain. Rare on the east Australian coast, Port Hacking, N.S.W., and New Guinea.

PYROPHACUS HOROLOGICUM var. STEINII Schiller

Fig. 84*b, c*

Pyrophacus horologicum var. *steinii* Schiller, 1937.

Shape as for type but with plate formula 6-7′ 12″ 12-12‴ 4-10⁗.

Distribution.—Warm-water form. Tropical Atlantic, Mediterranean, rare as a guest in North Atlantic to 61°N. (Gran 1912), rare, if ever, in Baltic (Paulsen 1913). Indian Ocean; Red Sea, West Indies, Celebes, Gulf of Siam, Singapore, South Pacific. Found on the east coast of Australia from Cape Pillar, Tas., to New Guinea, and in the St. Vincent's and Spencer Gulfs, S.A. In the Sydney region frequently occurs with the type form.

Genus HEMIDINIUM Stein

Hemidinium Stein, 1883.

Body asymmetrically elliptical, dorsoventrally more or less constricted. Girdle incomplete, about ½ the circumference, forming a left spiral: sulcus well developed; shell with 17 thin plates, with or without chromatophores; no stigma. Type species *H. nasutum* Stein.

HEMIDINIUM NASUTUM Stein

Fig. 85

Hemidinium nasutum Stein, 1883.

Body asymmetrically oval. Girdle median, a descending left spiral of $\frac{1}{2}$ a turn. Sulcus confined to hypocone, reaching posterior margin. Chromatophores yellow or brown. Nucleus posterior. Length 24-48 μ.

Distribution.—Fresh water from Tyrol to Finland. Brackish water in Finland; salt lakes near Odessa; Bosphorus. Australia: Port Hacking, N.S.W.

Family **PERIDINIIDAE** Kofoid

Genus DIPLOPSALIS Bergh

Diplopsalis Bergh, 1882.

Cell lenticular to subspherical with conspicuous left longitudinal list extending past antapex. Apical pore present, on apical horn; girdle central, not displaced. Spines absent. Plates 3′-4′ 1*a*2*a*6″-7″ 5‴ 1-2⁗.

DIPLOPSALIS LENTICULA Bergh

Fig. 86*a-c*

Diplopsalis lenticula Bergh, 1882.
Glenodinium lenticula Schiller, 1937.

Cell obovate to lens-shaped, epitheca and hypotheca nearly equal. Small apical horn. Girdle almost central, not displaced, circular; list supported by fine spines. Sulcus usually reaching antapex, the left side with a prominent hyaline list, which projects basally to the right, resembling a spine. The 3 large apical plates meet at the pore, the anterior intercalary nearly pushing out the 3rd and 4th precingulars. Plasma pale pink. Theca finely punctured. Reproduction by spores (usually 2), which emerge from the theca by its opening at the girdle, 29-75 by 33-155 μ. Plate arrangement: 3′1*a* 6″ 5‴ 1⁗.

Distribution.—Widespread, eurythermic and euryhaline. Australia: east Australia, estuarine-neritic; Antarctic (B.A.N.Z.A.R.E.).

DIPLOPSALIS LENTICULA forma MINOR Paulsen

Fig. 87*a, b*

Diplopsalis lenticula forma *minor* Paulsen, 1907.
Diplopeltopsis minor (Paulsen) Pavillard, 1913; Lebour, 1922, 1925.
Diplopsalis sphaerica Meunier, 1910.
Peridinium lenticulatum Mangin, 1911.
P. paulseni Mangin, 1913.
P. lenticula Paulsen, 1912 partim.
Glenodinium lenticula forma *minor* Schiller, 1937; Ostenfeld, 1915.

Differs from type in the plate arrangement of the epitheca. This is 4′1*a* 7″5‴1⁗. The intercalary becomes an apical plate, and a 4-sided intercalary plate appears on the left side.

Distribution.—In brackish coastal water in all European seas. Australia: east coast in estuaries; Swan River, W.A.

DIPLOPSALIS ROTUNDATA (Lebour)

Fig. 88*a*, *b*

Peridiniopsis rotundata Lebour, 1922.
Peridinium limnophilum Lindemann, 1924.

Cell globular, tapering into a very short apical horn. Girdle central, not displaced, with conspicuous lists supported by spines. First apical pentagonal, like a meta *Peridinium*, anterior intercalary meeting it on left. Sulcus not reaching base of hypotheca and with a conspicuous wing on left projecting posteriorly. Plasma pinkish or almost colourless. Theca finely punctured, 22-28 μ. Plate formula 3′1*a*6″5‴2⁗.

Schiller (1937) placed *Diplopsalis* in *Glenodinium* together with *Peridiniopsis* Lebour, 1922, and *Diplopeltopsis* Pavillard, 1913. Paulsen (1949) considered *Diplopsalis* a valid genus. Schiller is doubtless correct in uniting the 3 genera as they are differentiated by a wandering anterior intercalary. *Peridiniopsis* and *Diplopeltopsis* therefore become *Diplopsalis*.

Distribution.—Plymouth; Australia: Port Hacking, N.S.W.; Swan River, W.A.

DIPLOPSALIS ORBICULARIS (Paulsen) Paulsen

Fig. 89

Diplopsalis orbicularis (Paulsen) Paulsen, 1949.
Peridinium orbiculare Paulsen, 1907, 1908.
Diplopsalopsis orbicularis (Paulsen) Lebour, 1925.
Diplopsalopsis orbicularis var. *temaris* Abé, 1927.

Cell globular or lens-shaped. Apical horn hardly apparent. Girdle central, not displaced. Lists without spines? Sulcus not reaching antapex, with a large wing on left protruding posteriorly. Plate formula of epitheca variable, 4′1 or 2*a* 7″5‴2⁗.

Distribution.—Neritic and estuarine. Eden, N.S.W., to north Queensland; Solomon Is.

Genus PERIDINIUM Ehrenberg

Peridinium Ehrenberg, 1832.

The classification of species within this genus is fraught with difficulty. Jörgensen (1923) divided the genus into sections and other authors have followed him while modifying certain sections. Taxonomic criteria are:

(1) Shape of body;
(2) Presence or absence of antapical horns;
(3) Shape of ventral plate (1st apical) of epitheca;
(4) Shape of 2nd intercalary plate:
  Ortho = 4-sided 1st apical,
  Meta = 5-sided 1st apical,
  Para = 6-sided 1st apical,

Quadra = 4-sided 2nd intercalary,
Penta = 5-sided 2nd intercalary,
Hexa = 6-sided 2nd intercalary,

(5) Number of intercalary plates on epitheca;
(6) Displacement of girdle;
(7) Hollowness of antapical horns;
(8) Apical horn "affixed" or tapering.

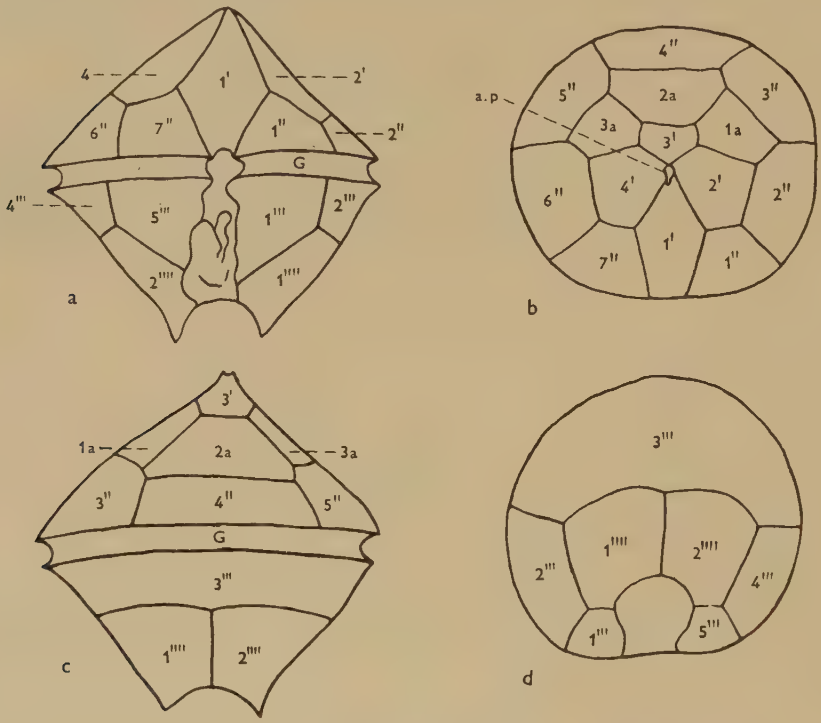

Fig. *D.*—Numbering of plates of *Peridinium* (after Lebour).

Criteria 1, 2, 6, and 8 are relatively constant for a species, although *Peridinium ovatum* may often be found without antapical horns and at times, where the girdle is normally slightly displaced, it may be circular in a number of examples, e.g. in *P. oceanicum*. The 1st apical plate of the epitheca varies to some extent, but seems constant enough to separate groups. The shape of the 2nd intercalary varies in the same species, e.g. *P. ovatum* may be quadra or penta. This does not seem to be very useful in defining groups or species. The number of intercalaries is also variable, though it may be a useful specific character.

Paulsen's (1949) groups are:

1. TABULATA Jörgensen

Rounded cells without horns, without or with small antapical spines. Girdle left-handed or circular, the apical furrow or groove including apical pore. Tabulation: ortho, penta, quadra, or hexa, 3 (rarely 2) intercalaries. (All freshwater species and some marine.) Gran and Braarud (1935) found that *P. americanum,* which is referred to this group, had 4 intercalaries.

2. AVELLANA Paulsen

Differs from (1) in the presence of an apical furrow, including apical pore, and having 2 intercalaries. Form rounded or quadrilateral.

3. MONOVELA Abé

Differs from 1 and 2 in having no horns but a conspicuous flagellar fin. The girdle is circular.

4. EXCENTRICA Paulsen

Cells globular or depressed, without spines. Girdle circular or left-handed. Two intercalaries, one much bigger than the other.

5. HUMILI-PIRIFORMIA Paulsen

Antapicals not hollow, cell depressed, girdle right-handed: often with 2 antapical spines, meta, quadra, penta, or hexa.

6. PELLUCIDA Jörgensen

Antapicals not hollow, cell ovoid and pointed or acuminate at top, rarely with "affixed" apical horn. Girdle right-handed; 2 antapical spines, often a 3rd on the left side as a continuation of the left edge of the sulcus. Para (rarely meta or ortho), usually hexa, rarely quadra or penta.

7. CONICA Jörgensen

Antapicals usually hollow, cell quadrangular or pentagonal in ventral view, no apical horn, girdle left-handed or circular. Ortho, hexa, penta, or quadra.

8. OCEANICA Jörgensen

Antapicals hollow, epitheca with concave sides tapering into apical horn: girdle left-handed, oblique. Ortho, quadra, may be penta or hexa (some authors show para).

9. DIVERGENTIA Jörgensen (including *Paradivergentia* Paulsen)

Antapicals hollow, often deeply indented base. Epitheca conical, may taper into an insignificant apical horn; meta, hexa, or quadra, 1 group para.

KEY TO SPECIES OF THE GENUS PERIDINIUM RECORDED IN THIS PAPER

Rounded cells without horns, with or without small antapical spines. Girdle left-handed or circular, apical furrow or groove including apical pore. Tabulation ortho, penta, quadra, or hexa, 3 (rarely 2) intercalaries. Includes all freshwater and some marine species .. *A.* TABULATA
(One species (*P. nudum*) recorded from Australia.)

Rounded or quadrilateral. Differs from Tabulata in having an apical furrow including apical pore, and having 2 intercalaries .. *B.* AVELLANA

Antapicals not hollow, cells depressed. Girdle right-handed; often with 2 antapical spines, meta, quadra, penta, or hexa .. .. *C.* HUMILI-PIRIFORMIA

Antapicals not hollow. Cell ovoid and pointed or acuminate at top, rarely with "affixed" apical horn. Girdle right-handed: 2 antapical spines, often a 3rd on left side as a continuation of left edge of sulcus. Para (rarely meta or ortho), usually hexa, rarely quadra or penta . *D.* PELLUCIDA

Antapicals hollow, often deeply indented base. Epitheca conical, may taper into insignificant apical horn. Meta, hexa, or quadra; 1 group para .. .. *E.* DIVERGENTIA

Antapicals usually hollow, cells quadrangular or pentagonal in ventral view; no apical horn; girdle left-handed or circular. Ortho hexa (may be penta or quadra) .. .. *F.* CONICA

Antapicals hollow, epitheca with concave sides tapering into apical horn; girdle left-handed, oblique. Ortho quadra, may be penta or hexa .. .. *G.* OCEANICA

B. AVELLANA

1. Cell biconical 2
Cell rhombic .. .. *P. thorianum*
Cell excentric, depressed .. .. *P. excentricum*
Cell spherical or oval 3
Cell pentagonal .. .. *P. africanum*
Cell with conical epitheca, rounded or slightly flattened hypotheca . *P. latum*
Cell with small apical horn .. .. *P. dakariensis*

2 (1). Epitheca approximately equal to hypotheca: sulcus curving strongly to left .. .. *P. abei*
Epitheca lower than hypotheca: sulcus straight, slightly displaced left .. .. *P. ventricum*

3 (1). "Comb" present on epitheca .. .. *P. willei*
Cell spherical, somewhat flattened ventrally, sulcus short .. .. .. *P. volzii*
Cell elongated oval 4
Cell ovate, somewhat angular. Sulcus strongly displaced; theca strongly and peculiarly reticulate .. .. *P. gatunense*

4 (3). Sulcus running ½ way up epitheca .. .. *P. striolatum*
Sulcus small but wide on epitheca 5
Sulcus poorly developed on hypotheca .. .. .. *P. gatunense* var. *zonatum*

5 (4). With spines 6
Without spines 7

6 (5). Strongly porulate .. .. *P. umbonatum*
Finely porulate .. .. *P. inconspicuum*

7 (5). Girdle subcircular .. .. *P. pusillum*
Girdle displaced strongly .. .. *P. centenniale*

C. HUMILI-PIRIFORMIA

1. Cell spherical or lenticular 2
Cell flat, ovate 4
Cell rhombic or pear-shaped, horn not affixed 6

2 (1). Apical horn "affixed" 3
Apical horn tapering 4

3 (2). Antapical spines present, not winged, at ends of sulcus .. .. .. *P. quarnerense*
Antapical spines present, not at end of sulcus .. .. *P. cerasus*
Antapical spines absent .. .. *P. globulus*

4 (2). Apical horn excentric; 1 antapical spine .. .. *P. monacanthum*
Apical horn regular 5
5 (4). Base flattened or rounded, with 2 blunt short humps .. .. .. *P. decipiens*
Base flattened or rounded, without humps, with or without 2 unwinged antapical spines .. .. *P. ovatum*
6 (1). Antapical spines not winged 7
Antapical spines winged 10
7 (6). Antapical spines not at ends of sulcus .. .. *P. roseum*
Antapical spines at end of sulcus 8
8 (7). Spines small or absent .. .. *P. brevipes*
Spines long 9
9 (8). Base indentate, apical spine tapering .. .. *P. mite*
Base flat, apical and antapicals very fine, "affixed" .. .. *P. obovatum*
10 (6). Spines very variable but not winged .. .. *P. granii*
Spines winged 11
11(10). Cell pear-shaped 12
Cell clumsily ovate, almost rectilinear .. .. *P. piriforme, P. breve**
12(11). Cell rounded, oval 13
Cell flask-shaped, narrow and long .. .. *P. ampulliforme*
13(12). Spines with very broad wings .. .. *P. latispinum*
Wings moderate .. .. *P. steinii*

D. Pellucida

1. Left sulcal list ending in broad wing, right ending in spine .. *P. curvipes*
Both sulcal lists ending in spines 2
Both sulcal lists recurved below apex .. .. *P. variegatum*
2 (1). Apical horn affixed 8
Apical horn not affixed 3
3 (2). Apical horn conical, small 4
Apical horn moderate .. .. *P. diabolus*
Apical horn long 7
4 (3). Right antapical unwinged 5
Right antapical winged 6
5 (4). Left antapical widely winged, cell smooth .. .. *P. hirobis*
Left antapical narrowly winged or wingless, cell appears wrinkled .. .. *P. okamurai*
6 (4). Epitheca conical, sides rectilinear .. .. *P. pallidum*
Epitheca subconical, sides convex .. .. *P. pellucidum*
7 (3). Moderate size; all horns much less than body length .. .. *P. pedunculatum*
Small body; all horns nearly or equal body length .. .. .. *P. tenuissimum*
8 (2). Left and right sulcal lists large, extended on to antapical spines . *P. sphaericum*
Sulcal lists narrow, right may be absent, only left extending on to antapical spine .. .. *P. ovum*

E. Divergentia

1. Tabulation para .. .. *P. solidicorne*
Tabulation meta or ortho 2
2 (1). Cell approximately as long as, or longer than, broad 3
Cell shorter than broad 8
3 (2). Epitheca convex 4
Epitheca concave 5
4 (3). Antapicals solid 9
Antapicals hollow .. .. *P. divergens*

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* *P. breve* is probably a form of *P. piriforme.*

5 (3). Antapicals spinulate, ortho 6
Antapicals not spinulate, meta .. .. *P. divergens*
6 (5). Epitheca tapering gently into apical horn .. .. *P. remotum*
Epitheca (and hypotheca) very shallow near girdle, curving sharply through 90° into horns 7
7 (6). Antapicals winged or reticulate .. .. *P. elegans*
Antapicals slightly unequal, smooth .. .. *P. grande*
8 (2). Right antapical longer than left; girdle sinuate .. .. *P. crassipes*
Left antapical longer than right; girdle nearly circular .. .. *P. curtipes*
9 (4). Antapicals equal .. .. *P. brochii*
Antapicals unequal .. .. *P. wiesneri*

F. CONICA

1. Cell broadly pentagonal .. .. *P. pentagonum*
Cell pyriform to polyhedral, epitheca quadrilateral in side view, shallow hypotheca .. .. *P. turbinatum*
Cell rhombic 2
2 (1). Sides of epitheca and hypotheca weakly convex, base flat or slightly concave .. .. *P. conicoides*, *P. subinerme*, *P. punctulatum*
Epitheca triangular 3
3 (2). Antapicals bent outwards at point .. .. *P. divaricatum*
Antapicals definitely incurved, left usually shorter than right .. .. *P. achromaticum*
Antapicals not bent outwards 4
4 (3). Antapicals conical, solid with no or small spines .. .. *P. conicum*
Antapicals with strong spines 5
5 (4). Cell small, contracted dorsoventrally .. .. *P. mariebourae*
Cell large, not contracted dorsoventrally .. .. *P. leonis*

G. OCEANICA

1. Cell equidimensional or slightly longer than broad 2
Cell much longer than broad 4
2 (1). Long axis very oblique .. .. *P. depressum*
Long axis moderately oblique 3
3 (2). Cell large; rounded rhombic .. .. *P. oblongum*
Cell small, sides sigmoid .. .. *P. claudicans*
4 (1). Horns conical, tapering, sides sigmoid .. .. *P. oceanicum*
Horns very long, narrowly tapering, sides rhombic .. .. *P. murrayi*

A. TABULATA

PERIDINIUM NUDUM Meunier

Fig. 90

Peridinium nudum Meunier, 1910.

Cell globular, slightly longer than broad, girdle slightly left-handed or circular, excavated, with narrow lists, not spinulate. Sulcus straight, hypotheca slightly bilobed. No antapical spines. First apical narrow with straight sides. Ortho, hexa: 3 intercalaries.

Distribution.—Belgian coastal water. Port Hacking, Sydney Harbour, N.S.W., estuarine.

B. AVELLANA

PERIDINIUM ABEI Paulsen

Fig. 91

Peridinium abei Paulsen, 1930.
P. biconicum Abé, 1927.

Cell biconical, longer than broad, epitheca approximately equals hypotheca, left-handed. Ventral groove including apical pore, girdle indented with narrow lists, sulcus deep, curving to the left, ending on left margin of hypotheca. Surface often punctulate; ortho; 2 intercalaries.

Distribution.—Mutsu Bay, Japan; Indian Ocean (Matzenauer 1933), Jervis Bay to Port Stephens, Port Hacking, N.S.W.; New Guinea; Swan River, W.A. A neritic and estuarine form, common at times.

PERIDINIUM THORIANUM Paulsen

Fig. 92

Peridinium thorianum Paulsen, 1905.
Properidinium thorianum Meunier, 1919.
Archaeperidinium thorianum Lebour, 1922.

Cell in ventral view with typical rhombic form and convex or almost straight sides. Circular from above. Girdle hollow, striped, displacement about 1 width to the left. Sulcus straight, narrow with lists, usually inermis. Clearly papillate surface. Yellow. The warm-water forms are lower and more contracted.

Distribution.—Barents Sea, Iceland, English Channel, Flemish coast near Niewport in brackish water. African coast; in warm water in the Atlantic and Indian Oceans. Euryhaline and eurythermic. Found in Port Hacking, N.S.W.

PERIDINIUM VENTRICUM Abé

Fig. 93*a, b*

Peridinium ventricum Abé, 1927.

Characteristic species, rather like *P. abei;* biconical; epitheca lower than hypotheca with straight or slightly concave sides. Hypotheca longer, tapering more gradually; girdle indented, left-handed; sulcus straight, displaced little to the left or not displaced, giving a slightly hollowed base contour. Ortho, 2 intercalaries. Apical pore slit-like, sculpture light: plate edges not as clearly marked as *P. abei,* from which it differs in the lower epitheca and straight sulcus.

Distribution.—Mutsu Bay, Japan in summer, Port Hacking and continental shelf of New South Wales.

EXCENTRICA

PERIDINIUM EXCENTRICUM Paulsen

Fig. 94*a, b*

Peridinium excentricum Paulsen, 1907.
Peridinium perrieri Fauré-Frémiet, 1909.
Archaeperidinium excentricum Lebour, 1922.

Cell depressed, very much obliquely twisted so that the left side of the hypotheca is larger than the right and the right longer than the left. Apex conical, eccentric; anterior intercalaries very dissimilar, the 1st small, the 2nd very large and reaching beyond the centre of the dorsal surface. Girdle circular, excavated, with lists supported by fine spines. Sulcus deep, oblique, reaching beyond base of hypotheca with narrow

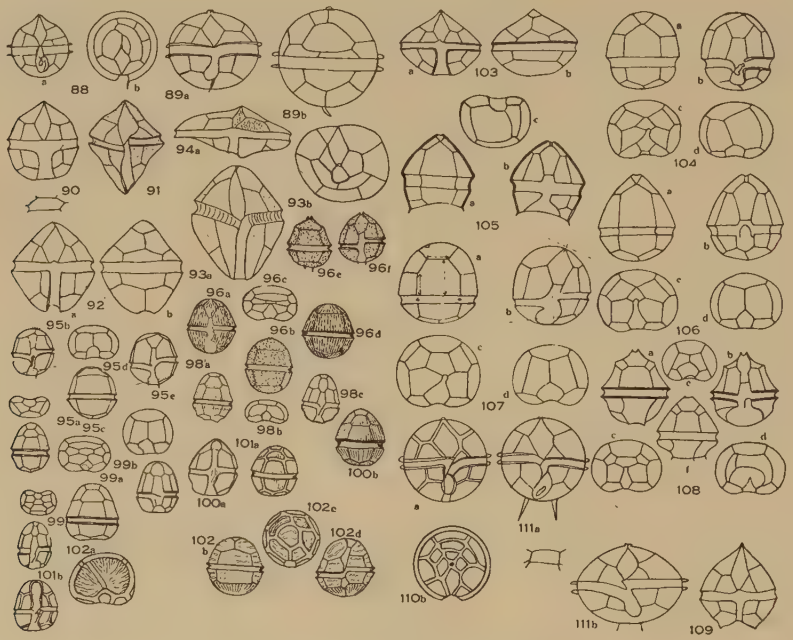


Fig. 88.—*Diplopsalis rotundata* (Lebour). *a*, Ventral view; *b*, epitheca. Port Hacking. Fig. 89.—*D. orbicularis* (Paulsen) Paulsen, 1949. *a*, Ventral; *b*, dorsal view. Port Hacking. Fig. 90.—*Peridinium nudum* Meunier, 1910. Port Hacking. Fig. 91.—*P. abei* Paulsen, 1930. Port Hacking. Fig. 92.—*P. thorianum* Paulsen, 1905. Port Hacking. Fig. 93.—*a*, *P. ventricum* Abé, 1927. Fig. 94.—*a*, *b*, *P. excentricum* Paulsen, 1907. Port Hacking. Fig. 95.—*a-e*, *P. volzii* Lemmermann, 1905 var. *botanicum* (Playfair) Lindemann, 1931. (After Playfair.). Fig. 96.—*a-f*, *P. volzii* forma *maeandricum* Lauterborn, 1910. (After Playfair.). Fig. 97.—*P. striolatum* Playfair, 1919. (After Playfair.). Fig. 98.—*a-c*, *P. striolatum* forma *rugosum* (Playfair) Lefèvre, 1932. (After Playfair.). Fig. 99.—*a*, *b*, *P. striolatum* forma *truncatum* (Playfair) Lefèvre, 1932. (After Playfair.). Fig. 100.—*a*, *b*, *P. striolatum* forma (Playfair) Lefèvre, 1932. (After Playfair.). Fig. 101.—*a*, *b*, *P. striolatum* forma *auburnense* (Playfair) Lefèvre, 1932. (After Playfair.). Fig. 102.—*a-d*, *P. gatunense* var. *zonatum* (Playfair) Lefèvre, 1952. (After Playfair.). Fig. 103.—*P. latum* Paulsen, 1908. Port Hacking. Fig. 104.—*a-d*, *P. umbonatum* Stein, 1883. (After Playfair.). Fig. 105.—*a-c*, *P. inconspicuum* Lemmermann, 1899. (After Playfair.). Fig. 106.—*a-d*, *P. pusillum* (Penard) Lemmermann, 1901. (After Playfair.). Fig. 107.—*a-d*, *P. centenniale* (Playfair) Lefèvre, 1932. (After Playfair.). Fig. 108.—*a-f*, *P. africanum* Lemmermann, 1907. (After Playfair.). Fig. 109.—*P. dakariensis* Dangeard, 1927. New Guinea. Fig. 110.—*P. globulus* Stein, 1883. Port Hacking. Fig. 111.—*P. quarnerense* Schröder, 1910. *a*, Jibbon Cape; *b*, Trial Bay.

lists. Hypotheca projecting on left in an antapical process. Colour pinkish. Diameter 45-50 μ.

Distribution.—North Sea, Mediterranean, Indian Ocean. Rare in Port Hacking, N.S.W.

PERIDINIUM VOLZII Lemmermann

Peridinium volzii Lemmermann, 1905.
P. guestrowense Lindemann, 1918, 1925; Lefèvre, 1932.
P. kincaidi Wailes, 1933.

Cell spherical, somewhat flattened ventrally, 36-80 μ long and about the same breadth. Very like *P. willei*, differing from it in the smaller ventral plate, the lack of "comb", and the short sulcus, which does not reach the lower end.

Distribution.—Europe in all lakes and marshes. Australia (Playfair 1919), Africa (Victoria Nyanza and Madagascar). Not found in this investigation.

PERIDINIUM VOLZII var. BOTANICUM (Playfair) Lindemann

Fig. 95*a-e*

Peridinium volzii var. *botanicum* (Playfair) Lindemann, 1931.
P. tabulatum Playfair, 1912,
P. willei var. *botanicum* Playfair, 1919; Lefevre, 1932.
P. willei var. *botanicum* Playfair, 1919; Lefèvre, 1932.
non *P. tabulatum* Claparède & Lachmann, 1899.

Characterized by 2 short antapical spines.

Distribution.—Australia, Malaya.

PERIDINIUM VOLZII forma MAEANDRICUM Lauterborn

Fig. 96*a-f*

Peridinium volzii forma *maeandricum* Lauterborn, 1910.
P. tabulatum var. *westii* forma *australis* Playfair, 1912; var. *hieroglyphicum* Playfair, 1912.
?P. hieroglyphicum Playfair, 1919.

Characterized by vermiform sculpture, often reticulate.

Distribution.—Germany, Switzerland, Tyrol, Australia: Sydney region, St. George's Basin, N.S.W.

PERIDINIUM STRIOLATUM Playfair

Fig. 97

Peridinium striolatum Playfair, 1919.

Cell elongated oval, flattened dorsoventrally, 42-52 μ long, 34-49 μ wide. Girdle slightly left-handed; sulcus running ½ way up the epitheca, strongly inclined at antapex. Epitheca much larger than hypotheca. Ventral plate hexagonal. Small. All plates areolate, ridged.

Distribution.—Australia: Sydney Harbour (Playfair 1919), St. George's Basin, N.S.W.

PERIDINIUM STRIOLATUM forma RUGOSUM (Playfair) Lefèvre

Fig. 98*a-c*

Peridinium striolatum forma *rugosum* (Playfair) Lefèvre, 1932.
P. striolatum var. *rugosum* Playfair, 1919.

Distinguished by plates of hypotheca and a punctulate line below girdle.

Distribution.—Australia (Port Jackson, N.S.W.) (Playfair 1919).

PERIDINIUM STRIOLATUM forma TRUNCATUM (Playfair) Lefèvre

Fig. 99*a, b*

Peridinuim striolatum forma *truncatum* (Playfair) Lefèvre, 1932.
P. striolatum var. *truncatum* Playfair, 1919.

Distinguished by the low, flattened hypotheca (fluctuation).

Distribution.—Sydney Harbour (Playfair 1919).

PERIDINIUM STRIOLATUM forma ACUMINATUM (Playfair) Lefèvre

Fig. 100*a, b*

Peridinium striolatum forma *acuminatum* (Playfair) Lefèvre, 1932.
P. striolatum var. *acuminatum* Playfair, 1919.

Epitheca ending in a blunt point.

Distribution.—Sydney Harbour (Playfair 1919).

PERIDINIUM STRIOLATUM forma AUBURNENSE (Playfair) Lefèvre

Fig. 101*a, b*

Peridinium striolatum forma *auburnense* (Playfair) Lefèvre, 1932.
P. striolatum var. *auburnense* Playfair, 1919.

Distinguished by areolation and parallel banded stripes.

Distribution.—Australia (Sydney, Auburn, Lismore, N.S.W.) (Playfair 1919). Schiller (1937) considered the separation of these varieties unwarranted.

PERIDINIUM GATUNENSE Nygaard

Peridinium gatunense Nygaard, 1925.
P. cinctum var. *gibbosum* Lefèvre, 1927.

Cell ovate, somewhat angular, apical flattened. Epitheca and hypotheca approximately equal: 45-80 by 55-80 μ. Sulcus strongly displaced with more or less prominent lists and deeply grooved girdle and sulcus. Yellow-brown chromatophores. Theca thick-walled, coarsely reticulate.

PERIDINIUM GATUNENSE var. ZONATUM (Playfair) Lefèvre

Fig. 102*a-d*

Peridinium gatunense var. *zonatum* (Playfair) Lefèvre, 1932.
P. tabulatum var. *zonatum* Playfair, 1912.
P. zonatum Playfair, 1919.

Cell rounded, elliptical. Epitheca larger than hypotheca. Sulcus only a little developed on hypotheca. Rough ridges scattered on surface arranged parallel to the sutures (relationships of this form are not clear).

Distribution.—Australia (Playfair 1919).

PERIDINIUM LATUM Paulsen

Fig. 103

Peridinium latum Paulsen, 1908.
Diplopsalis acuta (Apstein) Entz, 1904.
Glenodinium acuta Apstein, 1896; Lemmermann, 1910.
Entzia acuta (Apstein) Lebour, 1922, 1925; Schilling, 1913.

Epitheca regularly conical, sharply tapering at apex, giving a short apical horn. Hypotheca rounded, antapically often slightly flattened. Plate formula 4′ 1-2*a*, 7″, 5‴, 1⁗. Plasma chocolate-brown without chromatophores. 29-39 by 26-67 μ.

Distribution.—European ponds and lakes, also in brackish water. Australia: Port Hacking, N.S.W.

PERIDINIUM UMBONATUM Stein

Fig. 104*a-d*

Peridinium umbonatum Stein, 1883.
P. geminum Playfair, 1919.
P. caudatum Playfair var. *guildfordense* Playfair, 1919, and var. *planctonicum* Playfair, 1919.
P. lubieniense var. *inaequale* (Lef.) Lemmermann, 1928.
P. umbonatum var. *papilliferum* Lemmermann, 1908; Woloszynska, 1930.
P. linzium Lindemann, 1918.
P. ambiguum Lindemann, 1931.
P. umbonatum var. *spiniferum* Lefèvre, 1927.
P. umbonatum var. *inaequale* Lemmermann, 1910.
P. umbonatum var. *inaequale remotum* (Lemm.) Lefèvre, 1927.
P. umbonatum var. *contactum* (Stein) Lefèvre, 1927.
P. umbonatum var. *armatum* Lefèvre, 1927.
Glenodinium geminum (Playf.) Lindemann, 1931.
Glenodinium guildfordense (Playf.) Lindemann, 1931.

Cell elongate oval, 25-35 by 21-32 μ; somewhat flattened dorsoventrally. Epitheca wide, larger than hypotheca. Girdle with or without lists, relatively broad, ends displaced about ½ a width. Sulcus small but wide on epitheca, reaching antapex and then broad or only reaching the middle of hypotheca. Antapical region either flat-rounded or bordered by sulcus, sometimes with small and large spines. Theca with strong pores which are often arranged in lines. Chromatophores red-brown. Spores spherical or long with compact shell.

Distribution.—Cosmopolitan in ponds, marshes. More rarely in lakes in all continents, also in tropics. Recorded from Australia by Playfair (1919).

PERIDINIUM INCONSPICUUM Lemmermann
Fig. 105*a-c*

Peridinium inconspicuum Lemmermann, 1899.
P. minimum (Schilling) Woloszynska, 1916.
?*P. javanicum* Bernard, 1908.
P. munusculum Lindemann, 1918.
P. munusculum var. *contactum* Lindemann, 1918.
P. munusculum forma *spiniferum* Lindemann, 1918.
P. inconspicuum conjunctum (Lemmermann) Lefèvre, 1927.
P. inconspicuum var. *contactum* Lindemann, 1918.
P. inconspicuum remotum (Lemmermann) Lefèvre, 1927.
P. inconspicuum var. *armatum* Lemmermann, 1910.
P. inconspicuum forma *marchicum* (Lemmermann) Lindemann, 1918.
P. caudatum Playfair, 1919.
P. caudatum var. *morsum* Playfair, 1919.
P. caudatum var. *excavatum* and var. *angulosum* Playfair, 1919.
P. tabulatum var. *caudatum* Playfair, 1912.
P. marchicum Lemmermann, 1910; Schilling, 1913.
P. marchicum var. *ceyense* Nygaard, 1926.
P. inconspicuum var. *balatonicum* Entz, 1927.
P. steinmanni and var. *armatum* Woloszynska, 1930.
P. parvulum Woloszynska, 1930.

Cell oval, pointed at apex; slightly flattened in transverse view, 15-30 by 12-15 μ. Epitheca somewhat longer than hypotheca. Sulcus broad indented, with or without slight lists; only slightly displaced. Sulcus usually strongly widened below and always reaching antapex. Plates concave or convex. On hypotheca at plate corners are 3 more or less long spines, rarely more (forma *armatum*). Under strong magnification, fine, longitudinal rows of pores can be seen. Chromatophores seem to be rare. Spherical spores observed.

Distribution.—Apparently cosmopolitan in cold and temperate waters, Australia (Playfair 1919).

PERIDINIUM PUSILLUM (Penard) Lemmermann
Fig. 106*a-d*

Peridinium pusillum (Penard) Lemmermann, 1901.
P. orreri Huitfeldt-Kaas, 1900.
P. geminum var. *elegans* Playfair, 1919.
P. pusillum forma *gracile* Lefèvre, 1932.
Glenodinium pusillum Penard, 1891.
G. lefevrei Lindemann, 1928.

Cell elongate-oval, somewhat flattened ventrally, 18-25 by 13-20 μ. Epitheca more or less conical. Hypotheca smaller and shallow, dome-shaped. Girdle almost circular. Sulcus not quite reaching antapex. Plate junctions of hypotheca papillate, papillae may be present on the edges of the sulcus. Chromatophores yellow-brown. Spores conical.

Distribution.—Europe in ponds, lakes, and swamps. Also recorded from Australia and Africa.

PERIDINIUM CENTENNIALE (Playfair) Lefèvre

Fig. 107*a-d*

Peridinium centenniale (Playfair) Lefèvre, 1932.
P. umbonatum var. *centenniale* Playfair, 1919.
P. umbonatum var. *globosum* Lefèvre, 1927.
P. centenniale var. *fistulum* Lindemann, 1931.

Cell somewhat spherical, dorsoventrally slightly flattened, 28-43 by 25-40 μ. Girdle submedian, displaced at least a girdle width, edges very thick. Sulcus short or reaching antapex. Plates convex with irregular papillae.

Distribution.—Europe (France and Spain), Madagascar, Malaya, Australia.

PERIDINIUM AFRICANUM Lemmermann

Fig. 108*a-f*

Peridinium africanum Lemmermann, 1907.
P. intermedium Playfair and var. *conicum* Playfair, 1919.
P. ornamentosum Lindemann, 1931.
P. africanum var. *contactum* Lindemann, 1931.
P. africanum var. *javanicum*, var. *intermedium* forma *spinulosum*, and forma *tatricum* Lefèvre, 1932.
P. marchicum var. *javanica* Woloszynska, 1912.
P. tabulatum var. *intermedium* Playfair, 1912.
P. tatricum var. *spinulosa* Woloszynska, 1916.
P. tatricum Woloszynska, 1916.
Goniaulax jensenii Nygaard, 1926.

Cell in ventral view pentagonal, 25-40 by 23-35 μ. Epitheca conical, somewhat larger than hypotheca, antapical region straight or concave. Girdle almost circular. Sulcus strongly broadened below with a large spine at the right and a smaller one or a bunch of spines at the left edge. Lines of fine punctures often present on plates. Spores heart-shaped with a thick, smooth membrane.

Distribution.—Europe (Germany, France, and Poland), Africa (Lake Victoria, Madagascar), Malaya, Australia.

PERIDINIUM DAKARIENSIS P. Dangeard

Fig. 109

Peridinium dakariensis P. Dangeard, 1927.

Cell somewhat spherical, epitheca contracted into a very small apical horn; hypotheca subspherical, shallower than epitheca with concavity between the 2 small antapical spines. Girdle somewhat right-handed, indented, slight lists. Sulcus extending slightly into epitheca. Narrow in hypotheca. Meta, hexa.

Distribution.—One example recorded from NE. Africa. Rare in Port Hacking, N.S.W., and coastal New Guinea waters.

C. HUMILI-PIRIFORMIA Paulsen, 1949

PERIDINIUM GLOBULUS Stein

Fig. 110

Peridinium globulus Stein, 1883.
P. sphaericum Murray & Whitting, 1899.

Cell globular or lens-shaped, with a very short "affixed" apical horn hardly apparent. Girdle strongly right-handed, not excavated, with lists supported by spines. Sulcus narrow, running upwards onto epitheca, with inconspicuous lists. No antapical spines. Theca punctate. Intercalary striae usually broad. Meta, hexa (hepta). Length 50-78 μ.

Distribution.—Warm-water species, very widespread and numerous. Rare in North Atlantic, Spitzbergen, Mediterranean, Adriatic, Bosphorus? English Channel. Eastern Australia (probably oceanic) in this investigation, rarely in Fremantle Harbour, W.A., probably derived from a warm water mass farther westward; Port Fairy, Vic.

PERIDINIUM QUARNERENSE Schröder

Fig. 111

Peridinium quarnerense Schröder, 1910.
P. globulus Stein (partim).
P. spitzbergense Broch, 1910.
P. globulus Meunier, 1919.
P. patens Dangeard, 1927.
P. globulus var. *quarnerense* Schiller, 1937.

Cell globular, with small "affixed" apical horn and 2 antapical spines usually continuous with sulcal lists. Girdle not indented, with lists supported by spines. Right-handed. Sulcus curved or straight, wider at base, may reach antapex, when the sides and lists are continued into spines. If not, the spines are "affixed". Plates meta, quadra, or meta, penta, not so clearly demarcated as in *P. globulus*. The author agrees with Paulsen (1949) that Schiller (1937) was not justified in including *P. quarnerense* with *P. globulus*.

Distribution.—Warm-water species in all oceans and in the Mediterranean. Found on the east Australian coast from Trial Bay, N.S.W. north: oceanic, and in and outside Port Hacking, N.S.W., in winter, associated with other oceanic, tropical forms.

PERIDINIUM OVATUM (Pouchet) Schütt

Fig. 112*a-d*

Peridinium ovatum (Pouchet) Schütt, 1895.
P. lenticulatum Fauré-Frémiet, 1908.
Protoperidinium ovatum Pouchet, 1883; Meunier, 1919.
Peridinium globulus var. *ovatum* Schiller, 1937.

Cell lenticular. Epitheca low, dome-shaped, tapering sharply into a small apical horn (not "affixed"). Hypotheca low dome-shaped, normally with 2 small antapical spines. Girdle not depressed, slightly right-handed or straight, lists supported by spines. Sulcus subantapical or reaching antapex, lists present, right more developed. Theca porulate. Plates meta, quadra, or penta.

Distribution.—Interoceanic, euryhaline, eurythermic, in all oceans, including Antarctic. Oceanic and neritic. Eastern Australian waters from Eden, N.S.W., to Port Moresby, New Guinea; southern coast of Victoria and off Albany, W.A.

PERIDINIUM CERASUS Paulsen

Fig. 113*a, b*

Peridinium cerasus Paulsen, 1907.
P. globulus Meunier, 1919 (partim).

Cell spherical with a conspicuous but fairly long apical horn, girdle slightly right-handed. Two antapical spines not at margins of sulcus but unsymmetrically at a distance from it. Theca punctate. Plates—precingular 1″ very small in contrast with large 7″, meta quadra.

Distribution.—East Greenland, Barents Sea, Adriatic, Mediterranean, eastern Australia from Storm Bay, Tas., to New Guinea.

PERIDINIUM ROSEUM (Paulsen)

Fig. 114*a, b*

Peridinium roseum (Paulsen), 1949.
P. roseum Paulsen, 1904 (false delineata).

Cell in ventral view rounded or somewhat rhombic, tapering gradually above to a short apical horn. Girdle right-handed, not depressed, lists present. Sulcus broadening below, winged; wings not connected with spines. Theca smooth. Plates meta, quadra. A form similar in shape, size, and plate arrangement and with a right-handed girdle and broadened sulcus is common in Australian estuaries from Eden, N.S.W., to Moreton Bay, Queensland. The theca is smooth or porulate but both sulcal lists are developed and prolonged into spines. Paulsen (1949) amended his original description, but the identity of the form is still not clear. He placed it as a cold-water neritic species, but agreed that it has been recorded from Danish and Scottish waters and probably from the Skaggerrak. The form found in the present investigation may well be a new species, but undoubtedly belongs to the *humile-piriformia* section.

PERIDINIUM DECIPIENS Jörgensen

Peridinium decipiens Jörgensen, 1899.
P. dubium Broch, 1910?

Cell flat ovate, contour of epitheca S-shaped, hypotheca dish-shaped. Apex of low epitheca pyramidal. Base flattened or rounded with 2 blunt short humps. Sulcus depressed, slightly right-handed with broad lists. Plate arrangement little known. Girdle view rounded, kidney-shaped, 44-56 by 75-90 μ. Jörgensen and Paulsen placed this species in this section, which suggests that it is meta, quadra or meta, penta. The examples seen in the present investigation are meta, quadra, though Broch figures *P. dubium* as ortho, quadra.

Distribution.—North Sea, Atlantic coast of Norway, Arctic Ocean, neritic. In this investigation the form was found in estuarine and neritic environments from Maria I., Tas., to Moreton Bay, Queensland, and in Buka Strait, Solomon Is.

PERIDINIUM GRANII Ostenfeld
Fig. 116*a-c*

Peridinium granii Ostenfeld, 1906.
P. sp. Gran, 1903.
?*P. pellucidum* var. *a* Pouchet, 1882.
P. finlandicum Paulsen, 1907; Woloszynska, 1929.
P. divergens Levander, 1894; non Ehrenberg.
P. divergens var. *levanderi* Lemmermann, 1900.
P. calosum Jörgensen, 1913.
P. tenuicorne Mangin, 1913.
P. concavum Mangin, 1919.
P. pseudogranii Peters, 1930.

The cell form of this species is very variable and difficult to describe. The girdle is flat in individuals with a rounded, depressed in those with a wedge-shaped, girdle region. Paulsen speaks of 2 hollow protuberances each with a wingless spine. His diagrams show them developed almost to the form of horns. Meunier's figures also show strong variation. Here, as with Paulsen, the spines are shown now large and sharply affixed, now so small that they scarcely stand out, and the antapical processes appear as projecting horns (Peters 1928). Lebour's (1925) diagrams agree with this. The individuals from the Antarctic depicted by Peters show strongly developed spines. In a few cells also he recognizes a fine extension of protoplasm in the base of the horn-like processes. They are connected through the type of antapical horns. It must be adduced from this that this species shows a large variation in the antapical processes, since these can be developed as spines or horns or as intergrades between these. The dorsal plate 2*a* may be symmetrical or asymmetrical (Schiller 1937).

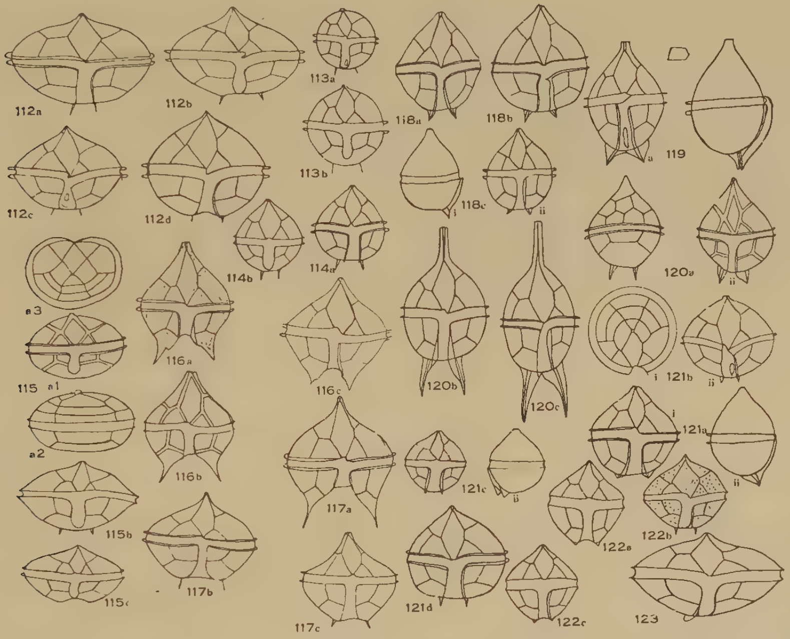
Distribution.—In cold and warm waters in all oceans, also in brackish water. Occurs from Port Hacking, N.S.W., to Moreton Bay, Queensland, on the east coast of Australia.

PERIDINIUM MITE Pavillard
Fig. 117

Peridinium mite Pavillard, 1916.
P. granii Paulsen, 1908; P. Dangeard, 1927; Matzenauer, 1933.

Schiller (1937) stated "The illustrations (pp. 190, 191, Schiller) show the unimportant differences from the type". Lebour also stated that "the chief differences between this species (*P. granii*) and *P. mite* consist in the shape of the cell and the hollow horns of *P. granii* compared with the long solid spines of *P. mite*". She recognized *P. mite* as different from *P. granii.* The latter was not found in any of the tropical stations on the Australian coast.

Distribution.—Jervis Bay, N.S.W., to Moreton Bay, Queensland; New Guinea, Antarctic (B.A.N.Z.A.R.E.).


112a
112b
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i
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a3
116a
115 a1
116c
120b
120c
i
121b
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116b
i
121a
ii
121c
ii
117a
115b
122a
122b
115c
117b
121d
117c
122c
123

Fig. 112.—*Peridinium ovatum* (Pouchet) Schütt, 1895. *a,* Port Hacking; *b,* B.A.N.Z.A.R.E. St. 100; *c,* B.A.N.Z.A.R.E. St. 104; *d,* St. 91. Fig. 113.—*P. cerasus* Paulsen, 1907. *a,* Port Hacking; *b,* Antarctic (B.A.N.Z.A.R.E.). Fig. 114.—*P. roseum* (Paulsen) Paulsen, 1949. *a,* Port Hacking; *b,* FSH58, B.A.N.Z.A.R.E. (Antarctic). Fig. 115.—*P. decipiens* Jörgensen, 1899. *a,* Trial Bay; *b, c,* Antarctic (B.A.N.Z.A.R.E.). Fig. 116.—*P. granii* Ostenfeld, 1906. *a, b, c,* Port Hacking. Fig. 117.—*P. mite* Pavillard, 1916. *a,* Port Hacking; *b, c,* South Tasman — convergence (B.A.N.Z.A.R.E.). Fig. 118.—*P. piriforme* Paulsen, 1904. *a,* Storm Bay; *b,* Heard I.; *c,* Antarctic (B.A.N.Z.A.R.E.). Fig. 119.—*P. latispinum* Mangin, 1926. Trial Bay. Fig. 120.—*a, P. steinii* Jörgensen, 1899. Trial Bay; *b, c, P. steinii* var. *mediterraneum* Kofoid, 1909; *b,* Storm Bay, Tasmania; *c,* Port Hacking. Fig. 121.—*P. breve* Paulsen, 1907. *a,* Trial Bay; *b,* Heard I.; *c,* FSN62; *d,* FSN25A, B.A.N.Z.A.R.E. Fig. 122.—*P. brevipes* Paulsen, 1908. *a,* Port Hacking; *b,* Heard I.; *c,* FSN22, B.A.N.Z.A.R.E. Fig. 123.—*P. monacanthum* Broch, 1910. Storm Bay, Tas.

PERIDINIUM PIRIFORME Paulsen

Fig. 118

Peridinium piriforme Paulsen, 1904.
P. steinii forma *pyriformis* Paulsen, 1905.

?*P. africanoides* Dangeard, 1927.
fide Paulsen, 1949.

Paulsen (1949) did not accept Schiller's (1937) clumping with regard to this species. He stated that *P. pyriforme* (Abé 1936) is a related form, but pear-shaped with acuminate epitheca; it comes near to *P. steinii* Jörgensen. His illustrations suggest that it might be an intergrade between *P. piriforme* Paulsen and *P. steinii*. The close relationship between the 2 species was recognized by Paulsen and by Lebour (1925).

Cell clumsily ovate, epitheca conical, almost rectilinear in outline, hypotheca dome-shaped, often with flattened sides and base. Spines short, winged, wing of left spine continuous with that of sulcus; girdle depressed, slightly right-handed. Sutures often very broad, surface of theca may be both striate and reticulate with pores in plate areoles, but none on sutures. Tabulation meta, penta.

Distribution.—A cool-water form. Iceland, Faroes, Shetlands, east Greenland, Cattegat, Antarctic. South-east Australia, Heard I. *P. piriforme* may well be a cool-water form of *P. steinii*.

PERIDINIUM LATISPINUM Mangin

Fig. 119

Peridinium latispinum Mangin, 1926.
?*P. sylvanae* Dangeard, 1927.
?*P. africanoides* Dangeard, 1927.

Cell in ventral view rounded oval, with an almost cylindrical short or rather long apical horn. Antapex with 2 broadly winged unequally large spines, the right larger than the left. Surface finely punctulate. 70-90 by 50-60 μ. Similar to *P. steinii*, closely related to *P. piriforme*, according to Schiller. Paulsen (1949) lists this species which is difficult to separate from *P. steinii* (both meta, penta), of which it is probably a form. Significantly it is recorded as a warm-water form in the Atlantic Ocean and in the present investigation it was found on 2 occasions amongst tropical forms (off Trial Bay, N.S.W.), including *Histioneis*, *Amphisolenia*, *Ceratium euarcuatum*, etc.

PERIDINIUM STEINII Jörgensen

Fig. 120*a*

Peridinium steinii Jörgensen, 1899.
P. michaelis Stein, 1883; Schütt, 1895; Ehrenberg, 1832; non Vanhöffen, 1897.
P. pellucidum Ramsay-Wright, 1907, non Bergh.
P. steinii subsp. *paulseni* Kofoid, 1909; Jörgensen, 1913.
?*P. micrapium* Meunier, 1919.
Protoperidinium pellucidum var. *B* Pouchet, 1883.

Cell pear-shaped. Hypotheca rounded, elongated apical horn. Girdle right-handed or circular, not excavated, with lists supported by fine spines. Two long solid antapical spines each with 3 fins, the left connected with lists of sulcus. Intercalary striae usually broad: tabulation meta, penta. Plasma colourless or pale pinkish, rarely yellowish. 39-52 by 22-40 μ, very variable.

Distribution.—Atlantic, Indian Ocean. Known from all European seas. Neritic, often numerous, east Australia: Eden, N.S.W.; to Solomon Is.; Storm Bay, Tas.; Port Phillip, Vic.; Fremantle, Geraldton, W.A.

PERIDINIUM STEINII var. MEDITERRANEUM Kofoid

Fig. 120*b*

Peridinium steinii var. *mediterraneum Kofoid*, 1909 (as subspecies).
P. longicollum Pavillard, 1916; Dangeard, 1927.

Differs only in a longer, thinner apical horn and longer spines 115-135 by 45 μ (body length 60 μ). Like *P. tenuissimum* Kofoid.

Distribution.—Mediterranean, Atlantic Ocean, warm water from east Australia and Storm Bay, Tas.

PERIDINIUM BREVE Paulsen

Fig. 121*a-d*

Peridinium breve Paulsen, 1907.
P. steinii forma *brevis* Paulsen, 1906.
?*P. styliferum* Schiller, 1929.
?*P. pedunculatum* Schütt, Schiller, 1920.

Cell clumsy, short ovate, thick-walled, sides somewhat rounded. Very short apical horn. Hypotheca rounded (usually somewhat irregularly, slightly flattened below). Girdle right-handed, only slightly excavated, with lists supported by spines. Sulcus broad, with inconspicuous lists ending in small slightly winged spines. Rarely the left list is not connected with the spine. Surface smooth or striped and reticulate. Intercalary striae usually broad, 44-75 μ. Paulsen (1949) considered that *P. breve* may be a form of *P. piriforme*.

Distribution.—Warm and cold regions of Atlantic and neighbouring seas, also in boreal regions; Australia: Port Hacking, N.S.W.; Antarctic.

PERIDINIUM BREVIPES Paulsen

Fig. 122

Peridinium brevipes Paulsen, 1908.
P. varicans Paulsen, 1911; Lebour, 1925; Woloszynska, 1929.
P. incurvum Lindemann, 1924.

Cell somewhat rhombic in outline, with rounded ends and conical apex. Girdle right-handed, excavated, with very narrow lists. Sulcus broadening towards antapex, ending in 2 small spines which may be absent. Plasma colourless. Tabulation meta, quadra, 18-36 μ.

Distribution.—Arctic conditions in North Sea and Baltic; neritic. Australia: Port Hacking, N.S.W.

PERIDINIUM MONACANTHUM Broch

Fig. 123

Peridinium monacanthum Broch, 1910.
P. complanatum Meunier, 1910.

Cell low, rather like *P. decipiens,* with epitheca with S-shaped sides and high, tapering excentric apical horn. Hypotheca dish-shaped, with 1 antapical spine to the right of the end of sulcus. Girdle right-handed, almost circular with smooth lists. L 40 μ. B 64 μ. Meta, quadra.

Distribution.—Spitzbergen; Australia: Storm Bay, Tas.; cold-water form.

New species — HUMILI-PIRIFORMIA

PERIDINIUM OBOVATUM sp. nov.

Fig. 159

A small species with a very low cake-shaped body; girdle not depressed, lists moderate, slightly right-handed. Sulcus narrow near girdle, very wide, circular on antapical surface, lists narrow. Characterized by long slender apical horn and antapical spines, the latter hair-like. Tabulation meta, quadra or hexa. Height of body 15 μ, breadth 55 μ, apical horn 20 μ, spines 20 μ.

Distribution.—Numerous in a number of plankton tows taken by B.A.N.Z.A.R.E. in Antarctic in 1930-31.

PERIDINIUM AMPULLIFORME sp. nov.

Fig. 160*a, b*

A small flask-shaped species. Epitheca narrowly conical, with tapering apical horn and concave sides, convex near girdle. Girdle slightly depressed, with lists, slightly right-handed. Hypotheca evenly rounded; sulcus flaring widely, right and left lists equally developed, concurrent with 2 long, slender, diverging spines. Tabulation meta, quadra. Length 40 μ, width at girdle 25 μ.

Distribution.—Estuarine. Port Hacking, N.S.W.; Swan River, W.A.

D. PELLUCIDA

PERIDINIUM CURVIPES Ostenfeld

Fig. 124

Peridinium curvipes Ostenfeld, 1906.
P. subcurvipes Lebour, 1923, 1925; P. Dangeard, 1927.

Rounded oval, length equal to or slightly less than breadth. Apical horn short. Girdle broadly winged, right-handed. Left sulcal list with broad wing, evenly curved posteriorly towards antapex. Right list narrower, ending in a spine, 1st apical more or less asymmetrical. Ventral plate arrangement very variable (ortho, meta, or para), 2*a* quadra or hexa. There seems to be a variation in tabulation exceeding that in *P. divergens* which Barrows (1918) and others have recorded (meta, para). Length 44-52 μ, breadth 44-46 μ.

Distribution.—From Greenland to tropical regions of the Atlantic; Mediterranean; Baltic; Antarctic (B.A.N.Z.A.R.E.).

PERIDINIUM DIABOLUS Cleve

Fig. 125

Peridinium diabolus Cleve, 1900.
P. formosum Pavillard, 1909; P. Dangeard, 1927; Lebour, 1925.
P. macrospinum Mangin, 1912; Lebour, 1925; Fauré-Frémiet, 1922.
P. longispinum Mangin, 1930.
P. pellucidum Carisso, 1911.
P. (divergens) longipes Karsten, 1907; Matzenauer, 1933; Pavillard, 1935.
?P. longicollum Pavillard, 1915, 1916; ?P. Dangeard, 1927.

Body rounded, little contracted dorsoventrally. Apical horn of moderate length, conical, epitheca sides S-shaped. Hypotheca rounded with a concave basal portion. Girdle slightly right-handed or circular, not excavated, lists supported by spines. Sulcus widening below, left edge with list ending in a spinelet connected with the winged left antapical spine. Right antapical spine winged, equal to left, both longer than $\frac{1}{2}$ a cell width. Total length 85-180 μ, breadth 35-75 μ.

Distribution.—Warm water, Atlantic and Indian Oceans, Mediterranean on coasts of England and Belgium. Australia, east coast, Eden, N.S.W., to Moreton Bay, Queensland. Antarctic convergence (B.A.N.Z.A.R.E.).

PERIDINIUM HIROBIS Abé

Fig. 126

Peridinium hirobis Abé, 1927.

Possibly identical with *P. pellucidum* (Schiller 1937).

Rounded cell with small tapering apical horn, more rounded than shown by Schiller for *P. pellucidum*. Girdle right-handed, not or slightly depressed, with wide lists. Sulcus wide, edged with lists, right continuous with unwinged antapical, left with a wide wing projecting below body connected to upper portion of antapical. Tabulation, para (meta according to Abé's diagram), hexa.

Distribution.—Japanese coast (Futagojima), Australia: Port Hacking, N.S.W.

PERIDINIUM OKAMURAI Abé

Fig. 127

Peridinium okamurai Abé, 1927.

Cell elongated pear-shaped, epitheca conical with convex sides and small apical horn. Hypotheca hemispherical. Girdle slightly depressed, with lists; right-handed. Sulcus with lists. Antapical horns with or without narrow wings. Sutures wide, may be slightly indented, giving a wrinkled appearance to the cell. Tabulation para, hexa, 59-75 by 38-50 μ.

Distribution.—Japan, Mutsu Bay; Australia: Moreton Bay, Queensland.

PERIDINIUM OVUM Schiller

Fig. 128

Peridinium ovum Schiller, 1911; non Mangin, 1912.
P. ellipsoideum Dangeard, 1927.
P. ellipsoides Dangeard, 1927.
?*P. rectum* (Kof.) Pavillard, 1916.
?*P. sphaericum* Okamura, 1912.
?*P. rectum* Kofoid, 1907.

Cell oval, almost spherical with small affixed apical horn and 2 long, unwinged or short, winged antapical spines. Girdle not depressed, narrow lists supported by fine spines. Sulcus wide, with lists, wide list on left side attached to antapical spine. Tabulation meta, hexa.

Distribution.—Mediterranean and warm water of Atlantic and Pacific Oceans. East coast of Australia, rare south of Trial Bay, N.S.W.

PERIDINIUM PALLIDUM Ostenfeld

Fig. 129*a, b*

Peridinium pallidum Ostenfeld, 1899.
P. pseudopallidum Peters, 1930.

Cell flattened dorsoventrally, somewhat rhombic in ventral view, longer than broad, apex conical. Girdle slightly right-handed, excavated, with lists supported by spines. Margins of sulcus ending in conspicuous winged spines, the right in 1, the left in 2. Theca finely dotted. Plasma yellowish green, usually with small yellowish green chromatophores. Probably holophytic. Intercalary striae narrow or broad, tabulation, para, hexa (quadra).

Distribution.—Atlantic, coast of Europe and Africa, Mediterranean, Arctic and Antarctic Oceans. Very numerous at Plymouth. Neritic and oceanic; eurythermic. Australia: rare — Port Hacking, N.S.W., to Queensland.

PERIDINIUM PEDUNCULATUM Schütt

Fig. 130

Peridinium pedunculatum Schütt, 1895.
?*P. pellucidum* Matzenauer, 1933.

The forms going under this name in the literature are morphologically very different, one of the reasons for this being that Schütt did not show the plate arrangement.

According to Paulsen (1908), this species is similar to *P. steinii* and *P. piriforme* but has a more conical epitheca, which suddenly contracts to a long apical horn, and the wing of the antapicals contracts suddenly at base. Schiller considered it a mixture of meta and para. The form ascribed by the author to *P. pedunculatum* resembles Schütt's and Matzenauer's illustrations rather than Jörgensen's.

Distribution.—Warm-water form from Atlantic, Mediterranean, and Indian Ocean. East Australia; Cape Pillar, Tas., to Solomon Is.; and Albany, W.A.

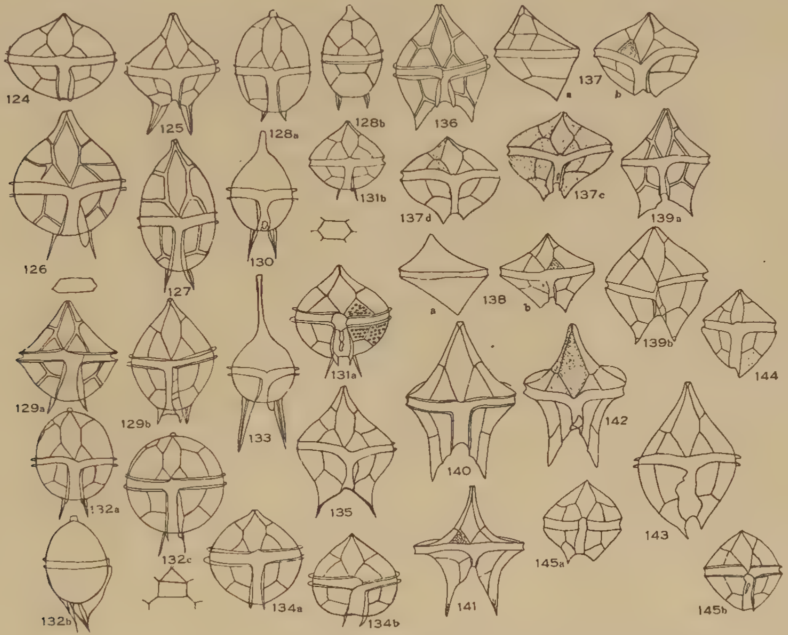


Fig. 124.—*Peridinium curvipes* Ostenfeld, 1906. FSN54, B.A.N.Z.A.R.E. Fig. 125.—*P. diabolus* Cleve, 1900. FSN17, B.A.N.Z.A.R.E. Fig. 126.—*P. hirobis* Abé, 1927. Port Hacking. Fig. 127.—*P. okamurai* Abé, 1927. Moreton Bay. Fig. 128.—*P. ovum* Schiller, 1911. *a*, Moreton Bay; *b*, Port Hacking. Fig. 129.—*P. pallidum* Ostenfeld, 1899. *a*, Sydney Harbour; *b*, var. *schilleri*, Tasmania, east coast (B.A.N.Z.A.R.E.). Fig. 130.—*P. pedunculatum* Schütt, 1895. Fig. 131.—*P. pellucidum* (Bergh) Schütt, 1895. *a*, Sydney Harbour; *b*, Antarctic (B.A.N.Z.A.R.E.). Fig. 132.—*a-c*, *P. sphaericum* Okamura, 1912. Port Hacking. Fig. 133.—*P. tenuissimum* Kofoid, 1907. Montague I. Fig. 134.—*P. variegatum* Peters, 1928. Antarctic (B.A.N.Z.A.R.E.). Fig. 135.—*P. solidicorne* Mangin, 1926. Port Hacking. Fig. 136.—*P. brochi* Kofoid & Swezy, 1921. Trial Bay. Fig. 137.—*P. crassipes* Kofoid, 1907. *a*, Lateral view; *b*, ventral view (Port Hacking); *c*, Heard I.; *d*, Antarctic (B.A.N.Z.A.R.E.). Fig. 138.—*P. curtipes* Paulsen, 1907. Port Hacking. Fig. 139.—*P. divergens* Ehrenberg, 1840. *a*, Sydney Harbour; *b*, Jibbon Cape. Fig. 140.—*P. remotum* Karsten, 1907. Trial Bay. Fig. 141.—*P. elegans* Cleve, 1900. Trial Bay. Fig. 142.—*P. grande* Kofoid, 1907. Trial Bay. Fig. 143.—*P. wiesneri* Schiller, 1911. Port Hacking. Fig. 144.—*P. achromaticum* Levander, 1902. Port Hacking. Fig. 145.—*P. conicoides* Paulsen, 1905. *a*, Jibbon Cape; *b*, Antarctic (B.A.N.Z.A.R.E.).

PERIDINIUM PELLUCIDUM (Bergh) Schütt

Fig. 131*a*, *b*

Peridinium pellucidum (Bergh) Schütt, 1895.
Protoperidinium pellucidum Bergh, 1881; non Pouchet, 1883; nec Vanhöffen, 1897.
Peridinium cavispinum Mangin, 1926.
P. huberi Schiller, 1929.

?*P. pedunculatum* Schütt, Schiller, 1929.
?*P. meunieri* Peters, 1930.

Cell very variable, very slightly flattened dorsoventrally, broadly oval. Long axis of girdle plane perpendicular. Girdle not or slightly excavated with lists supported by spines. Right margin of sulcus ending in 1, left in 2, antapical spines, all with or without hyaline wings. Colourless, pale pink or yellowish, 30-68 by 36-70 μ. Intercalary striae narrow or broad, theca finely reticulated, tabulation meta or para, hexa.

Distribution.—Common in estuaries along the east Australian coast.

PERIDINIUM SPHAERICUM Okamura

Fig. 132*a*-*c*

Peridinium sphaericum Okamura, 1912.
P. sphaeroidea Abé, 1927; P. Dangeard, 1927; Matzenauer, 1933.
P. globulus Stein, Karsten, 1907.
P. sphaericum var. *gracilis* Matzenauer, 1933.

Cell spherical or slightly oval with affixed apical horn and 2 winged antapical spines set well ventrally, lists on both sides of sulcus continuous with wings of spines. Girdle right-handed, not depressed, lists present. Tabulation para, quadra?

Distribution.—Interoceanic. Australia, east coast, Sydney Harbour, N.S.W.

PERIDINIUM TENUISSIMUM Kofoid

Fig. 133

Peridinium tenuissimum Kofoid, 1907.
P. steinii var. *elongata* Karsten, 1906.

A minute hyaline species related to *P. pedunculatum,* but distinguished by its smaller size, more elongated body, and longer apical horn and antapical spines; length of mid body greater than breadth. Mid body broadly ovoid and passes abruptly into cylindrical apical horn, which is nearly a diameter long, and flares slightly at apical pore. The acicular, divergent antapicals are nearly a diameter in length; girdle medium, not displaced. Lists of sulcus extend beyond base. Sutures very fine (not discernible, Kofoid). Meta, penta.

Distribution.—Tropical oceanic. East Australia: Eden, N.S.W., to Moreton Bay, Queensland.

PERIDINIUM VARIEGATUM Peters

Fig. 134*a*, *b*

Peridinium variegatum Peters, 1928.

Cell rounded pear-shaped to almost spherical, right-handed. Girdle lists broad, left and right sulcal lists recurved below antapex. Tabulation para, penta. 50-85 by 50-90 μ.

Distribution.—Antarctic, Weddell Sea (B.A.N.Z.A.R.E.).

E. DIVERGENTIA (including PARADIVERGENTIA)

PERIDINIUM SOLIDICORNE Mangin

Fig. 135

Peridinium solidicorne Mangin, 1926.
P. spiniferum Schiller, 1937 fide Paulsen, 1949.
P. spinosum Schiller, 1937.
P. areolatum Peters, 1928.
?*P. divergens pallidum* Karsten, 1906.

Cell like *P. brochii* but tabulation para, hexa. Surface areolate or spinulate.

Distribution.—Adriatic, Antarctic, Atlantic, and Indian Oceans. Mediterranean, Australia: Port Hacking, N.S.W.

PERIDINIUM BROCHII Kofoid & Swezy

Fig. 136

Peridinium brochii Kofoid & Swezy, 1921.
P. adriaticum Broch, 1910; Pavillard, 1916; Forti, 1922; Lebour 1925; Dangeard, 1927, 1932; non Schmarda, 1946.
P. divergens Lindemann, 1929; Abé, 1927.
P. divergens var. *adriaticum* Schiller, 1929.

Cell variable, approximately as long as broad, epitheca convex, tapering into a conical apical horn. Hypotheca convex, then concave tapering into 2 solid, diverging antapicals, base strongly concave. Girdle convex, with lists supported by spines, right-handed, lists continuing down broad sulcus extending below base of cell. Tabulation meta, quadra.

Distribution.—Atlantic Ocean and Mediterranean. Australia: east Coast, Trial Bay to Port Hacking, N.S.W.

PERIDINIUM BROCHII forma INFLATUM (Okamura) Schiller

Peridinium brochii forma *inflatum* (Okamura) Schiller, 1937.
P. inflatum Okamura, 1912.
P. crassum Dangeard, 1927; Matzenauer, 1933.

Somewhat broader than long, wider dorsally, humped, ventral surface of epitheca flattened in the upper ½, humped towards girdle. Right horn often longer.

Distribution.—Atlantic, Indian, and Pacific Oceans; Australia: Moreton Bay, Queensland; Garden I. and Port Hacking, N.S.W.

PERIDINIUM CRASSIPES Kofoid

Fig. 137*a-d*

Peridinium crassipes Kofoid, 1907.

A medium-sized species, with oblique girdle and short, stout antapicals. The body is low and stout, length 1.1 transdiameters. Slightly flattened dorsoventrally; it is excavated ventrally and has a reniform girdle section. Main axis deflected anterodorsally from perpendicular to girdle plane at an angle of 15°. Ventral face of both epitheca and hypotheca somewhat concave but dorsal convex. Apical horn conical, obtuse. Antapicals short and stout and close together. Antapicals characteristic, ending in a blunt semi-truncated projection with 2 or 3 principal points, 1 of which is homologous with tip of antapical, the other 2 representing respectively dorsal and ventral angles of the wide post margin, which is concave. Median points are posterior extensions of sulcal lists. Right antapical often longer than left. Sutures broad, surface areolated with nodal pores.

Schiller (1937), following Peters (1928), united *P. crassipes* and *P. curtipes*, but Paulsen (1949) disagreed with this. The author considers, with Paulsen, that the 2 species can be distinguished. In Australian waters, both forms occur at times, in the same plankton hauls, and can be separated. *P. curtipes* has a flatter girdle, is less heavily marked, and the sides, especially of the hypotheca, are much less convex and often concave.

Distribution.—In all oceans; subtropical, east Australia, Maria I., Tas., to Moreton Bay, Queensland; Albany, W.A.; Port Fairy, Vic.; oceanic to neritic, not estuarine; also Heard I. and Antarctic (B.A.N.Z.A.R.E.; Peters 1928).

PERIDINIUM CURTIPES Paulsen

Fig. 138

Peridinium curtipes Paulsen, 1907.

Very close to *P. crassipes* but distinguished by the almost circular girdle and more concave sides tapering rather suddenly into a conical apical horn. Left antapical usually longer than right.

Distribution.—A cool-water form, interoceanic, east Australia: Port Hacking, Coffs Harbour, N.S.W.; Moreton Bay, Queensland; Solomon Is., Bass Strait, near Victorian coast, estuarine.

PERIDINIUM DIVERGENS Ehrenberg

Fig. 139

Peridinium divergens Ehrenberg, 1840; non Schütt partim.
P. divergens var. *lenticulare* Ehrenberg, 1854.
P. lenticulare (Ehr.) Jörgensen, 1899 partim; Ramsay Wright, 1907.
P. divergens var. *bicuspidatum* Lemmermann, 1899.
?*Ceratium divergens* Claparède & Lachmann, 1859, 1861; ? Kent, 1881.
P. speciosum Jörgensen, 1912.
P. remotum Karsten, 1907 partim.
non *P. divergens* var. *adriaticum* Schiller, 1929 (= *P. brochii*).

A very variable form. Cell longer than broad, with 2 hollow antapical horns. Sides of epitheca concave or convex-concave, hypotheca concave. Girdle almost circular, slightly right-handed, slightly excavated with conspicuous lists supported by spines. Sulcus with lists extending into spinelets at bases of antapicals. Base concave, reticulate or spinulate.

Distribution.—Interoceanic, euryhaline. Australia: Maria I., Tas., to Queensland; South Australia; Albany, W.A.

PERIDINIUM REMOTUM Karsten

Fig. 140

Peridinium remotum Karsten, 1907; Matzenauer, 1933.

Epitheca conical, tapering, somewhat asymmetrically into the sharper cone of apical horn, with conical hypotheca projecting from the left-handed, depressed girdle. Antapicals strong, with strong outwardly directed spines on the outer sides. Hypotheca deeply notched by the short sulcus, its edges ending at the projecting corners of both horns. Plates finely and clearly reticulated. Tabulation ortho, quadra. 145 by 106 μ.

Distribution.—Indian Ocean, Australia: Port Hacking, Pittwater, N.S.W.; estuaries on east coast.

PERIDINIUM ELEGANS Cleve

Fig. 141

Peridinium elegans Cleve, 1900.
P. grande Dangeard, 1927; Paulsen, 1930.
P. fatulipes Okamura, 1912.

Cell with long, slender processes and a shallow body which is wedge-shaped to flat near girdle. Antapicals usually diverging at a sharp angle, the pointed ends often with rings and reticulate sculpture. 160-200 by 100-180 μ. Tabulation ortho, quadra.

Distribution.—Tropical, as a guest in subtropics. Australia: south-east coast.

PERIDINIUM GRANDE Kofoid

Fig. 142

Peridinium grande Kofoid, 1907.
P. elegans Matzenauer, 1933.
P. truncatum Graham, 1942.

A very large species of the *P. divergens* group with wide, flaring girdle and long horns. Body elongated (1.2-1.4 × diameter). Epitheca equals hypotheca. Girdle section strongly reniform. Epitheca a very low cone with a very flaring base and dorsally set tapering apical horn. Sides deeply concave. Hypotheca less abruptly contracted than epitheca. Antapicals slightly unequal, divergent, conical, acute. Base indentate, with nearly straight sides. Girdle narrow, median, nearly horizontal. Slightly left-handed, depressed, ribbed. Sulcus with low membranous lists projecting beyond base. Theca faintly reticulate with minute pores.

Distribution.—Tropical oceans. Mediterranean; east Australia, Eden, N.S.W., to north Queensland; south-central section of Great Australian Bight.

PERIDINIUM WIESNERI Schiller
Fig. 143

Peridinium wiesneri Schiller, 1911.
?*P. angustum* P. Dangeard, 1927.
P. pellucidum (Bergh) (Schütt) Matzenauer, 1933.

Cell broadly rounded, apex and antapex tapering. Ending above in a short horn, below left has a hollow horn, right only slightly developed, both with short or long spines. Girdle left-handed, not depressed, 2*a* quadra. 56-70 by 40-50 μ.

Distribution.—Adriatic; Atlantic; Australia: Port Hacking, N.S.W.

F. CONICA

PERIDINIUM ACHROMATICUM Levander
Fig. 144

Peridinium achromaticum Levander, 1902.

Cell rhombic, somewhat flattened dorsally, 28-48 by 24-40 μ. Girdle almost circular, sulcus edges raised, their ends rounded, at times with spines, saprophytic, spores spherical.

Ostenfeld found specimens with only 2 intercalary plates.

Distribution.—Brackish and fresh water. North Sea, Baltic coast water; Indian Ocean; Aral Sea; Australia: Port Hacking, N.S.W.

PERIDINIUM CONICOIDES Paulsen
Fig. 145

Peridinium conicoides Paulsen, 1905.
P. sp. Fauré-Frémiet, 1908.

Cell in ventral view somewhat rhombic, with weakly convex sides. Girdle almost circular, and median with narrow lists. Hypotheca ending in 2 short, hollow horns. Sulcus broadening posteriorly, on the left making a twist just below girdle sometimes with 2 spinelets near it. Nearly circular in girdle view. 48-60 μ. Tabulation ortho, hexa.

Distribution.—Arctic, neritic species in Atlantic, Australia: east coast, Port Hacking, N.S.W.; Albany Harbour, W.A.; Antarctic (B.A.N.Z.A.R.E.).

PERIDINIUM CONICUM (Gran) Ostenfeld & Schmidt

Peridinium conicum (Gran) Ostenfeld & Schmidt, 1900; non Meunier, 1910 (= *P. leonis*) non 1919.
P. acutangulum (Lemmermann) Jörgensen, 1913.
P. conicum var. *bilobata* (Meunier) Schiller, 1929.
P. intermedium Canderas, 1938.
P. conicum forma *ceylonica* Matzenauer, 1933.

Cell nearly symmetrical in ventral view, flattened dorsoventrally. Epitheca triangular, with straight or slightly convex sides. Hypotheca and epitheca subequal. Hypotheca with 2 hollow antapical horns full of protoplasm, without spines. Girdle almost circular, slightly left-handed, excavated, supported by narrow lists. Intercalary striae often broad, especially on sutures between 2nd and 3rd apicals and 2nd and 6th precingulars. These form 2 conspicuous ridges characteristic of this species and *P. pentagonum*. Sulcus reaching beyond centre of hypotheca with very inconspicuous lists. Theca finely reticulated. Colour pinkish to colourless; probably saprophytic. 70-80 μ. Ortho, hexa.

Distribution.—In cold and warm water in all oceans. Neritic and oceanic. Australia, estuarine and neritic. East coast, Port Hacking, N.S.W., to Moreton Bay, Queensland; Solomon Is.; Israelite Bay, Swan River, W.A.; South Australia.

PERIDINIUM CONICUM forma ASAMUSHI Abé
Fig. 146*b*

Peridinium conicum forma *asamushi* Abé, 1927.

Hypotheca with concave contour, narrower than epitheca. Antapicals plump, rounded, with deeper hollow between them. Plate 2*a* divided.

Distribution.—Japan, off east Australia, Port Hacking, N.S.W.

PERIDINIUM DIVARICATUM Meunier
Fig. 147

Peridinium divaricatum Meunier, 1919.
P. sp. Mangin, 1913.

Cell bilateral, about 50 μ long. Epitheca making an isosceles triangle. Hypotheca with straight sides, 2 hollows, more or less strongly diverging horns, between which is a deep and wide notch.

Distribution.—Belgian and English coast (brackish water); Australia: Port Hacking, N.S.W.

PERIDINIUM LEONIS Pavillard
Fig. 148*a-c*

Peridinium leonis Pavillard, 1916.
P. saltans Pavillard, 1915.
?*P. typus* Fauré-Frémiet, 1908.
P. conicum Meunier, 1919.
P. pentagonum Dangeard, 1926, non Gran.
P. striatum Böhm, 1931, non Ostenfeld & Schmidt, 1901.

Cell in ventral view rhombic, 65-95 by 75-80 μ. Contour more or less concave. Epitheca triangular, running to a point. Hypotheca with 2 blunt conical horns, ending in 2 short, more or less strong spines, with a deep notch between. Girdle more or less left-handed, and, according to Pavillard, more or less perpendicular to the long axis. This is not so, according to Meunier's, Dangeard's, and Paulsen's figures. Apical pore double and long with 2 small spine-like prominences at the corners of plate 3′. These serve as a support for a low, delicate wing membrane, which runs dorsally along the edge of plates 6″ and 4′ and 2′ and 2″ and touches the back of the pore. This membrane ceases about the sagittal plane. The lines behind these plates run in a zigzag, thereby differing from *P. conicum* and *P. pentagonum* in which they are straight, a good differential character. Plates reticulate, ridged, rough to spiny, more rarely striped. Similar to *P. conicum* and *P. pentagonum.*

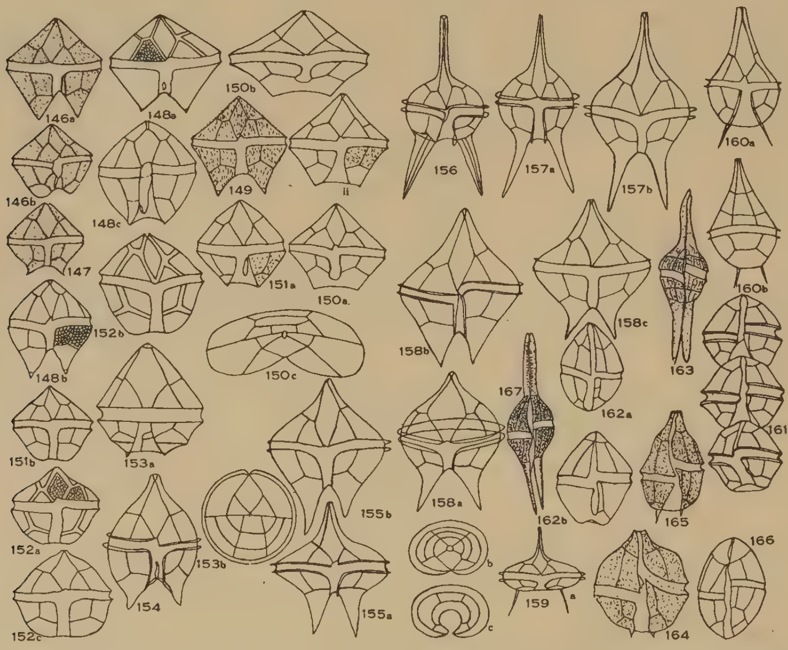


Fig. 146.—*a, Peridinium conicum* (Gran) Ostenfeld & Schmidt, 1901. Port Hacking; *b, P. conicum* forma *asamushi* Abé, 1927. Jervis Bay. Fig. 147.—*P. divaricatum* Meunier, 1919. Port Hacking. Fig. 148.—*a, P. leonis* Pavillard, 1916. Port Hacking; *b, c, P. leonis.* Moreton Bay. Fig. 149.—*P. marielebourae* Paulsen, 1930. Fig. 150.—*a, P. pentagonum* Gran, 1902; *b, P. pentagonum* var. *latissimum* Kofoid, 1907; *c, P. pentagonum* var. *latissimum,* girdle view. Fig. 151.—*P. subinerme* Paulsen, 1904. *a,* Port Hacking; *b,* Antarctic (B.A.N.Z.A.R.E.). Fig. 152.—*P. punctulatum* Paulsen, 1908. *a,* Port Hacking; *b,* Antarctic (convergence); *c,* Antarctic (B.A.N.Z.A.R.E.). Fig. 153.—*a, b, P. turbinatum* Mangin, 1926. *a,* Ventral view; *b,* epitheca. Fig. 154.—*P. claudicans* Paulsen, 1907. Port Hacking. Fig. 155.—*P. depressum* Bailey, 1855. *a,* Port Hacking; *b,* Antarctic convergence (B.A.N.Z.A.R.E.). Fig. 156.—*P. murrayi* Kofoid, 1907. Trial Bay. Fig. 157.—*P. oceanicum* Vanhöffen, 1897. *a,* Trial Bay; *b,* east Tasmania (B.A.N.Z.A.R.E.). Fig. 158.—*P. oblongum* (Aurivillius) Cleve, 1900. *a, c,* Antarctic (B.A.N.Z.A.R.E.); *b,* Jibbon Cape. Fig. 159.—*P. obovatum* sp. nov. Antarctic (B.A.N.Z.A.R.E.). *a,* Ventral view; *b,* epitheca; *c,* hypotheca. Fig. 160.—*P. ampulliforme* sp. nov. Port Hacking. *a,* Ventral; *b,* dorsal view. Fig. 161.—*Goniaulax conjuncta* sp. nov. Port Hacking. Fig. 162.—*a, b, G. apiculata* (Penard) Entz, 1904. Fig. 163.—*G. birostris* Stein, 1883. Trial Bay. Fig. 164.—*G. diegensis* Kofoid, 1911. Port Hacking. Fig. 165.—*G. digitale* (Pouchet) Kofoid, 1911. Port Hacking. Fig. 166.—*G. fragilis* (Schütt) *Kofoid,* 1911. Trial Bay. Fig. 167.—*G. glyptorhynchus* Murray & Whitting, 1899.

Distribution.—Atlantic Ocean, Indian Ocean, Australia: Moreton Bay, Queensland; Port Hacking, Eden, N.S.W.

PERIDINIUM MARIELEBOURAE Paulsen

Fig. 149

Peridinium marielebourae Paulsen, 1930.
P. obtusum Lebour, 1925; Fauré-Frémiet, 1908.
non *P. divergens obtusum* Karsten, 1906; Schiller, 1929.

Cell like *P. leonis,* but at most as large as the small individuals of this form, dorsoventrally somewhat contracted. Girdle circular or slightly left-handed, depressed, with and without spines in the lists. Hollow antapicals with 2 spines. Hull spiny or, according to Fauré-Frémiet, striped. Tabulation ortho, quadra (hexa, Fauré-Frémiet), plasma reddish, saprophytic, 50-55 μ.

Distribution.—Atlantic coast of Europe; Mediterranean; Indian Ocean; Australia: Port Hacking, N.S.W.

PERIDINIUM PENTAGONUM Gran

Fig. 150*a*

Peridinium pentagonum Gran, 1902.
P. sinuosum Lemmermann, 1905.
?P. divergens pentagonum Karsten, 1906.
?P. divergens var. *sinuosa* Lemmermann, 1899.

Cell asymmetric, pentagonal, right side smaller than left, dorsoventrally strongly contracted, 75-100 μ. Girdle median, more or less left-handed, curved, with prominent lists. Sulcus short, rounded below, often with a sharp border on right side, normally not reaching the end. Antapical horns more or less developed with 2 solid spines, between which is a shallow hollow with almost straight or somewhat irregular contour, or the hollow is deeper with almost crescent-shaped border, with yellow-brown chromatophores.

Distribution.—In cool and warm waters in all oceans. Often neritic. Euryhaline, eurythermic. Australia: neritic and estuarine. Eden, Cape Byron, N.S.W., on east coast; Port Phillip, Vic.; Swan River, W.A.; Solomon Is.

PERIDINIUM PENTAGONUM var. LATISSIMUM (Kofoid) Schiller

Fig. 150*b, c*

Peridinium pentagonum var. *latissimum* (Kofoid) Schiller, 1937.
P. latissimum Kofoid, 1907; Pavillard, 1931; Matzenauer, 1933.
P. pentagonum var. *depressum* Abé, 1927.

Dorsoventrally strongly constricted and deeply forked in middle, dorsally curved. Asymmetry also shown here, in that the right ½ is more or less larger than the left, 69-110 by 79-125 μ. Thickness 30 μ. Walls very thick, especially in antapical region. Ortho, hexa.

Distribution.—Pacific and Indian Oceans; coast of Japan. Warm water. Australia: an estuarine and neritic form on east coast of Australia and in Western Australia in Swan River. This variety often occurs with the type, but apparently without intergrades. At times one form or the other is present. It seems preferable to follow Schiller in regarding it as a form of *P. pentagonum.*

PERIDINIUM SUBINERME Paulsen

Fig. 151

Peridinium subinerme Paulsen, 1904.
?P. multistriatum Kofoid, 1907.
P. subinerme forma *asymmetrica* Matzenauer, 1933.

Cell bilaterally symmetrical, in girdle view nearly square, excavated at hind end. Epitheca with weakly convex sides; hypotheca with nearly straight sides. Girdle almost circular, excavated, supported by fine spines. Hind part of sulcus lying in a sharp depression whose borders coincide or nearly so, with sutures which lie around furrow, and which may bear spines. Intercalary striae sometimes broad. Theca usually reticulated or spiny. Paulsen (1949) states that in this species the epitheca is higher, and hypotheca more angular than in *P. punctulatum* while small spines are present. Tabulation is ortho, hexa, rarely penta. The writer concurs with this, as he had differentiated *P. subinerme* from *P. punctulatum* when they were found together and the differences agree with those set out by Paulsen.

Distribution.—Boreal or Arctic and cool-temperate form in Atlantic. In Australia, occurs in Albany, W.A.; Port Phillip, Vic.; and Port Hacking, N.S.W.; Antarctic and convergence (B.A.N.Z.A.R.E.).

PERIDINIUM PUNCTULATUM Paulsen

Fig. 152*a-c*

Peridinium punctulatum Paulsen, 1908.
P. subinerme var. *punctulatum* Schiller, 1937.

Shaped like *P. subinerme* but with lower epitheca and more rounded hypotheca. No spines on hypotheca and sulcus narrow. Theca finely punctured, may be spinulate but not reticulate. Girdle slightly left-handed, excavated, lists supported by fine spines, 40-72 μ. Tabulation ortho, penta, rarely hexa.

Distribution.—Cool-temperate Atlantic; Australia: neritic, estuarine; Port Hacking, N.S.W., to Moreton Bay, Queensland, on east; Albany to Israelite Bay on south-west coast of Australia. Spinulate forms seen in Port Hacking, N.S.W.

PERIDINIUM TURBINATUM Mangin

Fig. 153

Peridinium turbinatum Mangin, 1926.
P. inaequale Peters, 1928, non Fauré-Frémiet, 1908.

Cell pyriform to polyhedral. Epitheca conical, quadrilateral in side view. Girdle depressed, little displaced. Hypotheca very shallow, polyhedral with concave antapex with or without 2 short spinelets. Sutures raised. Tabulation ortho, quadra.

Distribution.—Antarctic. Occurs in Heard I. plankton and in B.A.N.Z.A.R.E. plankton.

G. OCEANICA

PERIDINIUM CLAUDICANS Paulsen

Fig. 154

Peridinium claudicans Paulsen, 1907.
P. sp. Fauré-Frémiet, 1908.
P. obliquum Dangeard, 1927; ?Matzenauer, 1933.
P. oceanicum forma *claudicans* Meunier, 1919.

Shaped like *P. oblongum,* of which it may be a neritic-estuarine form, but shorter and broader, with right antapical longer than left. Cell contents light yellow to colourless. Girdle left-handed, not or very slightly excavated with conspicuous lists. Tabulation ortho, quadra, penta, or hexa. Apical and antapical horns shorter and more conical than in *P. oblongum;* very similar in shape to *P. brochii* (meta).

Distribution.—In coastal waters of Europe, America, and the Indian Ocean. A brackish-water form of the Belgian and Dutch coasts. Australia: very widely distributed along the coast from Maria I., Tas., to New Guinea and Solomon Is.; Swan River and Albany, W.A.

PERIDINIUM DEPRESSUM Bailey

Fig. 155*a, b*

Peridinium depressum Bailey, 1855.
P. parallelum Broch, 1906; Broch, 1910; Paulsen, 1908.
P. divergens Vanhöffen, 1897; Meunier, 1910, 1919.
P. divergens var. *reniforme* Ehrenberg, 1854; Bergh, 1881; Pouchet, 1883.
P. divergens var. *typus* Pouchet, 1883.
P. divergens var. Schütt, 1895.
P. antarcticum Schimper, Karsten, 1905.
P. divergens var. *depressum* Aurivillius, 1899; Ostenfeld, 1899.
P. kofoidi Fauré-Frémiet, 1908.
?P. complanatum Karsten, 1905.
P. marinum Lindemann, 1925.

Cell short and broad, flattened obliquely dorsoventrally. Axis very oblique. Conspicuous apical horn. Girdle slightly left-handed, hardly excavated, with broad, membranous lists, strengthened with irregular spines. Hypotheca with 2 long, hollow antapical horns, each with a spinelet continuous with the sulcal lists. Theca reticulate, intercalary striae large or small, plasma pinkish, often with large oil globules. Pusule very large. Probably saprophytic. 116-114 by 116-200 μ. A very variable species, often confused with *P. divergens* Ehrenberg.

Distribution.—Euryhaline and eurythermal. Found from Antarctic to Arctic. Not observed in Bass Strait.

PERIDINIUM MURRAYI Kofoid

Fig. 156

Peridinium murrayi Kofoid, 1907.
P. murrayi var. *occidentalis* Pavillard, 1931.
P. divergens Ehrenberg, Murray & Whitting, 1899.
P. murrayi var. *orientalis* Matzenauer, 1933.

Probably a large growth form of *P. oceanicum,* from which it differs in its smaller, almost rhomboidal body, longer apical and antapical horns (the latter more strongly diverging), and the deep hollow between them. It is also less oblique than *P. oceanicum.*

Distribution.—Tropical in Mediterranean, Atlantic, Indian, and Pacific Oceans. Australia: Trial Bay, N.S.W.; Albany, W.A.

PERIDINIUM OCEANICUM Vanhöffen

Fig. 157*a, b*

Peridinium oceanicum Vanhöffen, 1897.
P. divergens var. *oceanicum* Aurivillius, 1898.
P. oceanicum forma *arupinensis* Broch, 1910.
P. elegans Cleve, 1900; Karsten, 1905.
P. divergens elegans Karsten, 1906.
P. divergens var. Bergh, 1881; Schütt, 1895; Murray & Whitting, 1899.
P. oceanicum var. *inaequipes* Mangin, 1930.
?P. obliquum Dangeard, Matzenauer, 1933.

Cells much more elongated and oblique than *P. depressum* with cell processes long and slender. Dorsoventrally flattened. Girdle oblique to sulcus, not depressed. Long axis often very considerably oblique. Sulcus usually with lists on each side, 118-200 μ long. Plasma violet-red. Tabulation ortho, quadra.

Distribution.—Oceanic, frequently a guest in neritic or estuarine waters. In all oceans and seas. Australia: east coast, St. Helens, Tas., to Solomon Is.; Port Phillip, Vic.; Albany, W.A.

PERIDINIUM OBLONGUM (Aurivillius) Cleve

Fig. 158*a-c*

Peridinium oblongum Cleve, 1900.
P. divergens var. *oblongum* Aurivillius, 1898.
P. oceanicum forma *oblonga* Broch, 1906.
P. oceanicum var. *oblongum* Paulsen, 1908.
P. oceanicum var. *parvulum* Mangin, 1913.
P. venustum Matzenauer, 1933.

Like *P. oceanicum,* but smaller, with less attenuated horns. Plasma pinkish, probably saprophytic. Tabulation ortho, quadra.

Distribution.—East Australia: Bass Strait to Solomon Is.; Albany, W.A.; Heard I. Neritic.

The author agrees with Paulsen (1949) in keeping separate the closely related species *P. claudicans*, *P. oceanicum*, *P. oblongum*, and *P. murrayi*.

Genus GONIAULAX Diesing

Goniaulax Diesing, 1866.

Variable in shape. Girdle about equatorial, left-handed, displaced from ½ to 7 times its width, sometimes with overhang. Plates 3′-5′, 0-2*a*6″ 6*g*6‴ 1*p* 1″″. Sulcus occupies whole ventral area, indented, consisting of 1 anterior, about 4 intermediate, and 1 posterior plates. First apical usually narrow, extending posteriorly to anterior plate of ventral area, with platelet covering apical pore. Plates porulate, often heavily ribbed. Theca divides obliquely in fission. Chains may be formed. Spores frequent. Chromatophores yellow to dark brown. Type species *G. spinifera* Diesing.

KEY TO SPECIES OF THE GENUS GONIAULAX RECORDED IN THIS PAPER

1.	Chain-forming	*G. conjuncta*
	Not chain-forming	2
2 (1).	Apical and antapical horns much longer than body	3
	Apical and antapical horns shorter than body	4
3 (2).	Body abruptly swollen	*G. birostris*
	Body oval	*G. glyptorhynchus*
4 (2).	Cell oval to spherical	5
	Cell elongate, pear shaped	*G. diacantha*
	Cell shape irregular-subangular	7
	Cell ovoid with conical, convex epitheca	*G. turbynei*
	Cell polygonal or rhombic	10
5 (4).	No apical horn, girdle premedian	*G. fragilis*
	Small apical horn	6
6 (5).	Girdle submedian, apical horn not oblique	*G. apiculata*
	Girdle median, apical horn oblique	*G. scrippsae*
7 (4).	Minute form, 21-28 by 14-22 µ	*G. minima*
	Small forms (40-80 µ), 2 or more antapical spines	8
	Medium to large form (more than 80 µ), 1 antapical spine	9
8 (7).	Body rotund, girdle displaced 3-6 widths, little overlap	*G. diegensis*
	Body longer than broad, girdle displaced 1-2 widths, overlap moderate	*G. digitale*
	Body subrotund, girdle displaced 2-3 widths, overlap large	*G. spinifera*
9 (7).	Medium forms, linear markings well developed	*G. polygramma*
	Large form, coarsely porulate, with linear markings	*G. kofoidii*
	Very large form, moderately porulate, linear markings not well developed; hypotheca J-shaped on left side	*G. pacifica*
10 (4).	Cell rhombic in ventral view	*G. hyalina*
	Cell polyhedral	11
11 (10).	No antapical spines	*G. polyedra*
	One antapical spine	*G. monacantha*
	Two small antapical spines	*G. alaskensis*

GONIAULAX CONJUNCTA sp. nov.

Fig. 161

A chain-forming species of *Goniaulax* related to *G. catenata* and *G. series*. Differs from the former in being inermis and having a blunt apex, and from the latter in not having a continuous protoplast, while the cells are of equal size.

Cell polyhedral with rounded angles, epitheca and hypotheca subequal. Epitheca and hypotheca flattened. Antapex of basal cell of chain slightly indented. Girdle depressed, displaced ½-1 width. Sulcus shallow, flaring slightly, straight. Plate formula 4′0*a* 6″ 6‴, 1*p* 1⁗.

Distribution.—Occurred abundantly at the Ballast Heap, Port Hacking, N.S.W. on 26.ii.45 and appeared in the plankton there for about a week. This was the only appearance of this organism in Port Hacking plankton between 1938 and 1951, although weekly phytoplankton townettings were made for a great part of this time.

GONIAULAX APICULATA (Penard) Entz

Fig. 162

Goniaulax apiculata Entz, 1904.
Peridinium apiculatum Penard, 1891.
G. clevei Ostenfeld, 1901.
G. apiculata var. *clevei* Ostenfeld, 1908.
G. polonica Woloszynska, 1916.
G. limnetica Lindemann, 1918.
G. austriaca Schiller, 1926.

Cell oval to spherical, with a small apical horn. Epitheca broadly rounded or angular oblong, in this case contracting to a blunt apical horn, longer than the broad, rounded hypotheca. Girdle slightly submedian, not overlapping, displaced about a girdle width. Lists very small. Sulcus broad, slightly or not twisted, lists present, toothed and supported by spines. Theca reticulate. Plate formula 4′, 0*a* (or 3, 1*a*) 6″6‴ 1*p* 1⁗; 30-60 μ. Holophytic.

Distribution.—A freshwater form, rare in brackish water. Also in the Aral Sea. Australia: Port Hacking and Jibbon Stations, N.S.W.; Moreton Bay, Queensland.

GONIAULAX BIROSTRIS Stein

Fig. 163

Goniaulax birostris Stein, 1883.

Body elongated, spindle-shaped, with abruptly swollen mid body, both ends projecting into 2 long horns. Length 130 μ, breadth 40 μ (calculated). Surface areolate.

Distribution.—A very rare species, pelagic, warm-water form. Known from the Mediterranean, Indian, Atlantic, and Pacific Oceans. Australia: east coast off Trial Bay, N.S.W., Port Fairy, Vic., Southern Ocean (August 1952).

GONIAULAX DIEGENSIS Kofoid

Fig. 164

Goniaulax diegensis Kofoid, 1911.
Gonyaulax spinifera Schütt, 1895.

A large, robust species, with a short, stout apical horn, elongated apex, 2 or 3 antapical horns, widely displaced (3-6 widths), girdle with little overhang. Sulcus not abruptly widened opposite distal end of girdle. Apical 4 separable. Reticulate surface, with wide, reticulate intercalary bands.

Distribution.—English Channel, Californian coast. Australia: estuarine and neritic, east coast, Port Hacking, Trial Bay, N.S.W., Moreton Bay, Queensland; New Guinea—west coast. Swan River, W.A.

GONIAULAX DIGITALE (Pouchet) Kofoid

Fig. 165

Goniaulax digitale Kofoid, 1911.
Protoperidinium digitale Pouchet, 1883.
Goniaulax spinifera Stein, 1883; Schütt, 1887, 1895; van Bremen, 1905; Entz, 1907, 1909; Paulsen, 1907, 1908.
G. granii Henkel, 1909.
Peridinium digitale Lemmermann, 1899.

Larger than *G. spinifera*, less rotund, with less overhang. Epitheca subconical, shoulders often slightly angled, generally 2 stout antapical spines. Lines joining ends of girdle make an angle of 13-18° with major axis, longitudinal furrow not abruptly widened opposite distal end of girdle, surface usually heavily reticulated. Plate formula $3'0a\ 6''\ 6\ 6'''\ 1p\ 1''''$.

Kofoid (1911) distinguished this species from *G. spinifera* by (1) size (a very doubtful character), (2) antapical spines (variable), (3) angle of line joining girdle ends major axis, (4) displacement of girdle, (5) overhang of girdle ends, and (6) shape of longitudinal furrow. Of these, the only characters readily usable are displacement of girdle and the widening of the sulcus opposite distal end of the girdle in *C. spinifera*. From diagrams in the literature, including those given in Schiller (1937), the last word has not yet been said on the separation of these 2 species. The author has found forms referable to both species in association with each other and with *G. diegensis*.

G. digitale is more abundant than *G. spinifera* in Sydney Harbour, N.S.W., while in the Swan River, W.A., *G. spinifera* predominates, with *G. diegensis* quite plentiful.

In the light of this and of the confusion of these 3 species in the literature, it seems probable that they are forms rather than species.

Distribution.—European coastal waters; Mediterranean; throughout the Atlantic Ocean; in coastal regions in the Pacific. Australia: east coast, Eden, Port Hacking, Trial Bay, N.S.W.; east Bass Strait; Moreton Bay, Queensland; Swan River, W.A.

GONIAULAX FRAGILIS (Schütt) Kofoid

Fig. 166

Goniaulax fragilis Kofoid, 1911.
Steiniella fragilis Schütt, 1895, 1896; Ostenfeld, 1900; Paulsen, 1908; Cleve, 1910; Schröder, 1900; Entz, 1902; Forti, 1922.

Body rotund, somewhat elongated, slightly flattened on ventral face. Epitheca and hypotheca subequal, no apical horn. Hypotheca sac-like, abruptly and asymmetrically rounded at antapex, left side being slightly fuller, girdle slightly premedian, displaced 3 widths without overhang, furrow not deeply impressed, no lists. Sulcus widening posteriorly. 85-105 by 65-80 μ.

Distribution.—Atlantic Ocean, Mediterranean, Pacific Ocean. Warm-water form. Australia: Port Hacking region, N.S.W.

GONIAULAX GLYPTORHYNCHUS Murray & Whitting

Fig. 167

Goniaulax glyptorhynchus Murray & Whitting, 1899.

Cell ovate, apical constricted to a long winged apical horn with elements easily splitting. Antapical even longer.

Distribution.—Tropical Atlantic between Barbados and Azores. Australia; east coast, Ulladulla and Crowdy Head, N.S.W.

GONIAULAX KOFOIDI Pavillard

Fig. 168*a-c*

Goniaulax kofoidi Pavillard, 1909.
?G. globosa Stüwe, 1909.

A large species with elongated body 1.65 diameters, tapering apical horn, asymmetrical antapex, and prominent left antapical spine, with coarsely porulate, longitudinally striate surface. Girdle section subcircular, flattened ventrally. Epitheca conical, slight angulation on left shoulder and abruptly changing into tapering apical horn with blunt apex. Hypotheca with almost straight sides and obliquely truncate antapex, lower than epitheca. Girdle displaced 2 widths, not overlapping. Single, winged antapical spine.

Distribution.—Atlantic, Mediterranean, Californian coast. Australia: tropical water off Trial Bay, N.S.W.; south of Port Fairy, Vic.; Southern Ocean.

GONIAULAX MONACANTHA Pavillard

Fig. 169*a, b*

Goniaulax monacantha Pavillard, 1916.

Cell polyhedral. Epitheca irregularly conical, asymmetrically tapering into a pointed apical horn, somewhat longer than hypotheca, which is sharply truncate at right, with 1 winged, well-developed spine. Girdle strongly hollowed, edges somewhat protruding, without membrane, displaced at least 3 times width. Theca with coarse pores, mostly in rows. Sulcus from lower side of girdle, broadening below with strong, toothed wings; 45-80 by 34-60 μ.

Distribution.—Gulf of Lyons. Australia: Port Hacking, N.S.W.

GONIAULAX PACIFICA Kofoid

Fig. 170*a*, *b*

Goniaulax pacifica Kofoid, 1907.
Steiniella cornuta Karsten, 1907.

An exceedingly large species resembling *G. polygramma* Stein, asymmetrically flattened and excavated on the ventral face, in ventral view more rounded, especially on post margin, than *G. kofoidi,* linear markings less regular and usually less developed than in *G. polygramma.* Posterior intercalary very narrow, its length 5-7 times width. Proximal end of girdle curved posteriorly.

Distribution.—Atlantic; Mediterranean; Indian and Pacific Oceans. Australia: east coast, Eden, N.S.W., to Moreton Bay, Queensland; Southern Ocean, Port Fairy, Vic.

GONIAULAX POLYEDRA Stein

Fig. 171*a*, *b*

Goniaulax polyedra Stein, 1883.
non Okamura, 1907 (= *Goniodoma acuminatum* Stein).

Body small, angular, polyhedral with ridges along sutures. Girdle equatorial, displaced 1-2 widths. Surface regularly pitted, rugose; 4 apical and 2 intercalary plates, the right apical 4′ minute.

Distribution.—Warm-water species (causes "red water" at times). Rarely in Australian waters—Port Hacking, N.S.W.

GONIAULAX POLYGRAMMA Stein

Fig. 172*a*-*c*

Goniaulax polygramma Stein, 1883.
G. schuetti Lemmermann, 1899.
Protoperidinium pyrophorum Pouchet, 1893.
Peridinium pyrophorum Lemmermann, 1889.

A medium-sized species of slightly elongated form (length 1.5-2 diameters), ventrally somewhat flattened. Epitheca somewhat conical, rather angular, tapering to a broad blunt apical horn. Girdle postmedian, ends displaced at most 2 widths, deeply indented with projecting edges, rarely with narrow lists. Sulcus narrow, strongly widened below, with 1 or more antapical spines (rarely absent), which are joined by a membrane. Theca with longitudinal lines, reticulate with numerous pores. Plate formula 3′ 0*a* 6″6‴ 1*p* 1⁗; chromatophores numerous.

Distribution.—In all tropical and subtropical waters in all oceans. Neritic and oceanic. Rare in cold water. East coast of Australia, common in Port Hacking, N.S.W., at times; south of Port Fairy, Vic.; Southern Ocean.

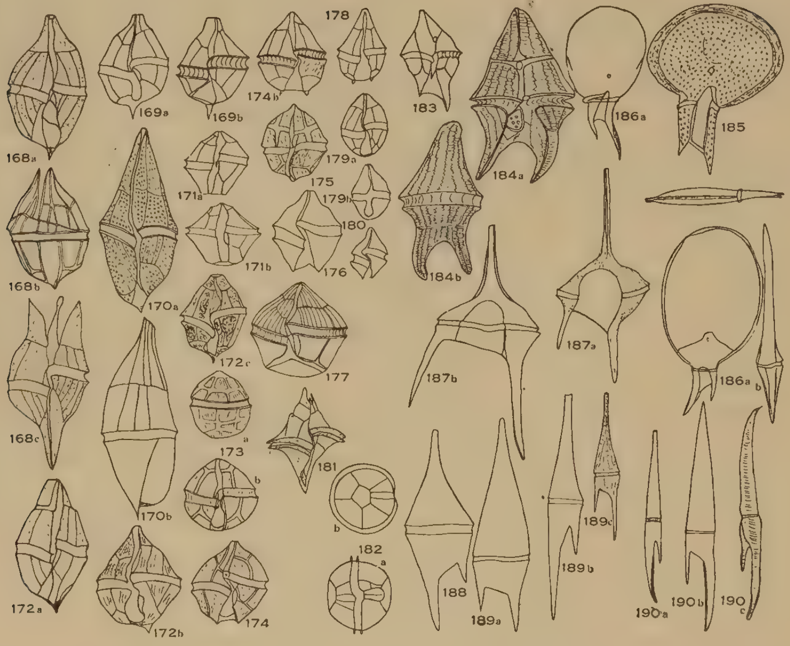


Fig. 168.—*Goniaulax kofoidi* Pavillard, 1909. *a*, Port Hacking; *b*, Queensland coast, *c*, Trial Bay. Fig. 169.—*G. monacantha* Pavillard, 1916. Fig. 170.—*G. pacifica* Kofoid, 1907. *a*, Trial Bay; *b*, Port Hacking. Fig. 171.—*G. polyedra* Stein, 1883. *a*, Trial Bay; *b*, east Tasmania (B.A.N.Z.A.R.E.). Fig. 172.—*a-c*, *G. polygramma* Stein, 1883. Port Hacking. Fig. 173.—*G. scrippsae* Kofoid, 1911. *a*, Swan River, W.A.; *b*,

Fig. 174.—*G. spinifera* (Claparède & Lachmann) Diesing, 1866. *a*, Swan River; *b*, Antarctic (B.A.N.Z.A.R.E.). Fig. 175.—*G. turbynei* Murray & Whitting, 1899. Port Phillip. Fig. 176.—*G. alaskensis* Kofoid, 1911. Antarctic, B.A.N.Z.A.R.E. Fig. 177.—*G. hyalina* Ostenfeld & Schmidt, 1901. Trial Bay. Fig. 178.—*G. diacantha* (Meunier) Schiller, 1937. Port Hacking. Fig. 179.—*G. minima* Matzenauer, 1933. *a*, Port Hacking; *b*, south-west of Albany (B.A.N.Z.A.R.E.). Fig. 180.—*G.* sp. Port Hacking. Fig. 181.—*Spiraulax jolliffei* (Murray & Whitting) Kofoid, 1911. Fig. 182.—*Protoceratium reticulatum* (Claparède & Lachmann) Butschli, 1885. Port Hacking. Fig. 183.—*Heterodinium dispar* Kofoid & Adamson, 1933. East Tasmania (B.A.N.Z.A.R.E.). Fig. 184.—*H. blackmani* (Murray & Whitting) Kofoid, 1906. Fig. 185.—*Ceratium cephalotum* (Lemmermann) Jörgensen, 1911. Trial Bay. Fig. 186.—*a-c*, *C. gravidum* Gourret, 1883, showing variation in antapicals. Port Hacking and Trial Bay. Fig. 187.—*a*, *C. candelabrum* forma *curvatulum* Jörgensen, 1920. Eden; *b*, *C. candelabrum* forma *depressum* (Pouchet). Jervis Bay. Fig. 188.—*C. hirundinella* (O. F. Müller) Bergh. Type *brachyceroides*. Swan River. Fig. 189.—*a*, *C. furca* (Ehrenberg) Claparède & Lachmann, 1859, var. *berghii* Lemmermann, 1900. Port Hacking; *c*, *C. furca* var. *eugrammum* (Ehrenberg) Jörgensen, 1911. Port Hacking. Fig. 190.—*C. incisum* (Karsten) Jörgensen, 1911. *a*, Port Hacking; *b*, Jervis Bay; *c*, Trial Bay.

GONIAULAX SCRIPPSAE Kofoid
Fig. 173

Goniaulax scrippsae Kofoid, 1911.

Body subspheroidal, epitheca subhemispherical, contracted abruptly at apex into a short apical horn with an oblique apex. Hypotheca hemispherical, inermis. Girdle equatorial, displaced 2-3 widths, overhang 0.1-1 width, indented, ridged. Sulcus deep, sigmoid, rather narrow, end rounded. Theca marked with fine subparallel lines which may be punctate, sometimes reticulate.

Distribution.—Atlantic, English Channel, Mediterranean, Californian coast. Australia: Sydney Harbour, Port Hacking, N.S.W.; Swan River, W.A.

GONIAULAX SPINIFERA (Claparède & Lachmann) Diesing
Fig. 174

Goniaulax spinifera (Claparède & Lachmann) Diesing, 1866.
Gonyaulax sp. van Breemen, 1905.
G. levanderi (Lemm.) Paulsen, 1907, 1908; Ostenfeld, 1908; Woloszynska, 1928.
G. mangini Fauré-Frémiet, 1908.
G. spinifera var. *levanderi* (Pauls.) Lindemann, 1924.
Peridinium spiniferum Claparède & Lachmann, 1858-9.
P. sp. Levander, 1894.
P. vexans Murray & Whitting, 1899.
Ceratocorys spinifera Schröder, 1906.
?*G. alaskensis* Kofoid, 1911.

A small rotund species, somewhat elongated anteriorly, with relatively wide, oblique girdle, with ridges and considerable overhang. Hypotheca with convex sides, with or without 2 or more small spines. Longitudinal furrow not flaring much posteriorly, often abruptly widened opposite distal end of girdle. Line joining ends of girdle makes an angle of 27-40° with major axis. Surface lightly marked. Length 24-50 μ.

Distribution.—Interoceanic. Also in brackish water. Australia: numerous in Port Hacking, Sydney Harbour, N.S.W.; and Swan River, W.A. In Sydney Harbour it forms almost the sole constituent of the phytoplankton at times, turning the water yellowish green. Antarctic (B.A.N.Z.A.R.E.).

GONIAULAX TURBYNEI Murray & Whitting
Fig. 175

Goniaulax turbynei Murray & Whitting, 1899.
?*Glenodinium ovatum* Fauré-Frémiet, 1908.

A small ovoid species with circular girdle section. Epitheca and hypotheca subequal; epitheca a low cone with convex sides, no apical horn. Apical region elliptical, flattened, sloping ventrally. Hypotheca subhemispherical with very slight ventral depression. Girdle equatorial, displaced 1-1.5 widths, very little, if any, overhang, deeply impressed, without lists or ridges. Sulcus, anterior part much restricted, middle region very narrow, and posterior part elliptical. Surface strongly marked with prominent longitudinal striae, standing out from the minor meshwork.

Distribution.—Tropical Atlantic ocean, in warm water of the Pacific Ocean, Mediterranean; Swan River, W.A.; Port Hacking, N.S.W.

GONIAULAX ALASKENSIS Kofoid
Fig. 176

Goniaulax alaskensis Kofoid, 1911.

Body in ventral view almost rhombic, with irregularly curved contour. Apex bent dorsally. Antapex slightly hollowed by sulcus with 2 spines at the end of sulcal lists. Girdle displaced about 4 widths, broad, deep, with projecting edges and lists. Sulcus sharply widened from girdle, flaring to the full width of antapex, lower edge with a ribbed ring. Theca delicately reticulate, with straight or slightly sinuous longitudinal striae. Holophytic, 65-77 by 65-74 μ.

Distribution.—Pacific Ocean from California to Alaska; Atlantic on Canadian coast. Antarctic (B.A.N.Z.A.R.E.).

GONIAULAX HYALINA Ostenfeld & Schmidt
Fig. 177

Goniaulax hyalina Ostenfeld & Schmidt, 1901.

Resembles *G. turbynei* in longitudinal striations. Differs in rhombic ventral view (not oval). Girdle rather narrow and clearly ribbed. Sulcus broader and more differentiated on hypotheca, *c.* 100 μ.

Distribution.—Northern region of Atlantic; east Australian coast.

GONIAULAX DIACANTHA (Meunier) Schiller
Fig. 178

Goniaulax diacantha (Meunier) Schiller, 1937.
Amylax diacantha Meunier, 1919.

Body elongate pear-shaped, dorsoventrally constricted. Epitheca conical with almost straight or slightly curved sides, hypotheca rather round. Sulcus straight or slightly curved anteriorly, widening posteriorly, reaching antapex. Margins sinuate, sulcal lists ending in 2 spines, 40 by 24 μ.

Distribution.—Nieuport Harbour, Belgium; brackish water, Port Hacking, N.S.W.

GONIAULAX MINIMA Matzenauer
Fig. 179

Goniaulax minima Matzenauer, 1933.
Glenodinium trochoideum Stein (Kleps, 1884).

A minute species with oval or subovate body, tapering anteriorly, girdle displaced about ½ a width, not or slightly overlapping. Sulcus nearly straight, widened somewhat posteriorly, not reaching antapex. Antapex rounded without spines. 21-28 by 14-22 μ.

Distribution.—Indian Ocean (numerous in nannoplankton), Port Hacking, N.S.W.; Indian Ocean south-west of Albany, W.A. (B.A.N.Z.A.R.E.).

GONIAULAX sp.

Fig. 180

A minute hyaline form with conical epitheca, bending slightly left. Margin concave, convex near girdle. Hypotheca truncate-conical, margins slightly concave; girdle wide, depressed, displaced 2-3 girdle widths, overlapping about 2 widths. Sulcus curved in epitheca, narrow, wedge-shaped in hypotheca reaching antapex, margins continued as 2 small spines, 30 by 20 μ. Theca hyaline. Plates could not be seen.

Distribution.—Port Hacking, N.S.W., common at times.

Genus SPIRAULAX Kofoid

Spiraulax Kofoid, 1911.

Very close to *Goniaulax*, differing only in that the uppermost plate of the sulcus does not touch the 1st apical, i.e. the sulcus does not invade the epitheca. Type species *S. jollifei* (M. & W.) Kofoid.

SPIRAULAX JOLLIFEI (Murray & Whitting) Kofoid

Fig. 181

Spiraulax jollifei (Murray & Whitting) Kofoid, 1911.
Gonyaulax jollifei Murray & Whitting, 1899; Schröder, 1900; Karsten, 1907.

A stout species, body very broadly and somewhat irregularly fusiform, of medium size, epitheca and hypotheca subequal, subconical, apex truncated, girdle displaced 3 widths. Plates 4′1*a* 6″6‴ 1*p* 1⁗. Girdle lists low. Surface coarsely pitted. Antapex terminating in a symmetrical, stout, acute, solid horn.

Distribution.—Warm water in all oceans and offshoots. Australia: tropical water on east coast of New South Wales as far south as Eden. Rare.

Genus PROTOCERATIUM Bergh

Protoceratium Bergh (1881).

Cell a somewhat angular oval or sphere. Girdle equatorial or slightly in front of the centre. Theca strongly reticulated so as to obscure the plates, sometimes with spines at the intersection of the meshes. Intercalary bands sometimes very broad. Plate formula 2′6″6‴1*p* 1⁗ or it is possible that there are 3 antapicals, which may merge into the ventral area, but the 1st formula seems to be the more probable. There is no apparent apical pore. One species — *Protoceratium reticulatum* (Claparède and Lachmann).

PROTOCERATIUM RETICULATUM (Claparède & Lachmann) Butschli

Fig. 182

Protoceratium reticulatum (Claparède & Lachmann) Butschli, 1885.
Peridinium reticulatum Claparède & Lachmann, 1859.
Protoceratium aceros Bergh, 1881.
Clathrocysta reticulata (Claparède & Lachmann) Stein, 1883.
Protoceratium splendens Meunier, 1910.

Epitheca and hypotheca subequal or hypotheca slightly longer. Rounded, angular. Girdle left-handed, displaced about a girdle width, with narrow lists supported by spines. Ventral area not quite reaching antapex, with very inconspicuous lists to sulcus. Theca strongly reticulate, often with apicules. Intercalary bands present or absent. First apical very narrow, 2nd polygonal, occupying anterior end. Six large precingulars. Girdle apparently not divided. Hypotheca with 6 postcingulars, 1st shorter with a small posterior intercalary behind it. Two long plates occupying most of ventral area and indenting antapical. Theca possibly to be regarded as antapicals. Plates very difficult to see on account of reticulation. 28-56 μ. Braarud (1945) has shown that certain Trochischia forms are really cysts of this form.

Distribution.—Neritic-estuarine. Very common northern species in Atlantic, Bosphorus, and Adriatic. Australia: Port Hacking, the Spit (Port Jackson), N.S.W.; Tinderbox, Storm Bay, Tas.; rare but may be numerous in single samples.

Family **HETERODINIIDAE** Lindemann, 1928

Genus HETERODINIUM Kofoid

Heterodinium Kofoid, 1906.

Body usually slightly asymmetrical, strongly flattened dorsoventrally, or sphaeroidal; with 2 large antapical horns or spines; girdle submedian, lacking or partly lacking post angular ridge; without lists; sulcus short and very narrow groove; reniform or circular pore present in characteristic ventral area at the meeting of the midventral and apical precingular sulcus of epitheca. Plate formula $3'1a'6''6$ or 7? $7'''$ $3''''$. Theca characteristically reticulate and porulate. Kofoid and Adamson (1933) recorded the genus only between 80 and 330 m and none from surface tows; according to these authors the horizontal distribution is restricted to tropical and subtropical seas with a minimum surface temperature above 18.9°C. In this investigation, 3 species were found at stations in the Southern Ocean with surface temperatures of 12.9-13.1°C between 100 and 0 m.

HETERODINIUM DISPAR Kofoid & Adamson

Fig. 183

Heterodinium dispar Kofoid & Adamson, 1933.

A small stout species with globose mid body, length 1.5 transdiameters; epitheca 0.62 transdiameter high, midventral suture very angled, ventral pore large; antapicals very unequal, right sometimes hardly developed; post margin obliquely asymmetrical. Surface sparsely porulate, sutures faint, with a loose reticulation only on left ventral face of epitheca. Length 72 μ.

The above is Kofoid & Atwood's description, but the term "globose" hardly fits their diagrams, which show a conical epitheca with slightly concave sides and a trapezoidal hypotheca, again with concave ventral contours.

Distribution.—Rare in eastern tropical Pacific and Galapagos and Easter Is. eddies and in the south equatorial drift. Australia: east of Eddystone, Tas. (B.A.N.Z.A.R.E.).

HETERODINIUM BLACKMANI (Murray & Whitting) Kofoid

Fig. 184*a*, *b*

Heterodinium blackmani (Murray & Whitting) Kofoid, 1906.
Peridinium blackmani Murray & Whitting, 1899.
H. curvatum Kofoid, 1907; Kofoid & Adamson, 1933.
Peridinium pulchrum Hensen, 1911 partim.

A very large, stout, handsome species, with an elongated body, much expanded at the girdle. Epitheca asymmetrically conical with a straight or slightly concave left and a more concave right margin, a blunt, rounded apex, and a slight flare at the girdle. No differentiated apical horn in ventral view but in lateral view there is a distinct constriction. Girdle postmedian, slightly displaced, ridged on both sides. Hypotheca asymmetrically subconical, sides concave with a deep sulcal excavation. Antapical horns subconical with a prominent midventral ridge, the left being rather sharply incurved at the distal end. Plates divided by prominent ribs, surface heavily reticulated with elongated polygons.

Kofoid divided *H. curvatum* from *H. blackmani*, but Schiller (1937) united them. He pointed out, with justification, that the differences are minor ones, and as the species had only been recorded by Murray and Whitting (1899), Kofoid (1907), and Karsten (1907), with a limited number of specimens, it seems desirable to follow Schiller's example. The example isolated in this investigation resembled Kofoid and Adamson's description and plates of *H. curvatum*. It occurred off Trial Bay, N.S.W.

HETERODINIUM DOMA (Murray & Whitting) Kofoid

Heterodinium doma (Murray & Whitting) Kofoid, 1906.
Peridinium doma Murray & Whitting, 1899.

A medium-sized spheroidal species without horns or spines; epitheca flattened ventrally; hypotheca hemispherical with trace of flattening at antapex. Girdle wide, without posterior rim, furrow scarcely indented; surface reticulate, spinous. Length 80 μ.

Distribution.—Rare in eastern tropical Pacific, Mexican current, Easter I. eddy, and south equatorial drift. Southern Ocean, west of King I. (one station, temp. 13.1°C to 100 m).

HETERODINIUM SCRIPPSI Kofoid

Heterodinium scrippsi Kofoid, 1906.

A medium-sized species of robust, angular habit; epitheca considerably larger than hypotheca with slightly emergent horn; anterior intercalary near girdle facing on precingular 3″; sutures often with ribbed lists, ventral pore at anterior end of ventral area. Length 130-155 μ.

Distribution.—Eastern tropical Pacific, California current, and tropical Atlantic. Southern Ocean south of Port Fairy, Vic. (temp. 13.1°C to 100 m).

HETERODINIUM ASYMMETRICUM Kofoid & Adamson

Heterodinium asymmetricum Kofoid & Adamson, 1933.

A small, rather clumsily formed, asymmetrical species with stout body; epitheca broadly and asymmetrically rounded; antapical horns very short, very unequal, the right scarcely developed; girdle oblique with undeveloped postcingular rim; surface smooth or with only a few scattered pores. Length 85-90 μ.

Distribution.—Rare in eastern tropical Pacific in Easter I. eddy and south equatorial drift. Southern Ocean south of Port Fairy, Vic., and west of King I. (6 specimens from 2 stations, temp. 12.9-13.1°C).

Family **CERATIIDAE**

Genus CERATIUM Schrank

Ceratium Schrank, 1795.

Cell usually flattened dorsoventrally, drawn out into hollow horns (usually 3). Girdle left-handed, usually with lists. Theca composed of plates. Plate formula 4′5″5‴2″″, ventral area of several plates taking up greater part of ventral face; sulcus in its left side with flagellar pore. Epitheca with long apical horn and pore at top; hypotheca typically drawn out into 2 hollow antapical horns, left horn formed by the 2 antapical plates, the right by postcingulars 4 and 5. Chromatophores numerous, yellow. Reproduction by oblique fission: spore formation rare. Chains occur and may be heteromorphic. Type species *C. hirundinella* (O. F. Müller) Bergh.

KEY TO SPECIES OF THE GENUS CERATIUM DESCRIBED IN THIS PAPER

1.	No apical horn. Subgenus *Archaeceratium*	2
	Apical horn present; epitheca and hypotheca of equal width; 2 or 3 closed antapicals directed rearwards, the right smaller than the left. Subgenus *Biceratium*	3
	Apical horn present: epitheca wider than hypotheca. Subgenus *Amphiceratium*	14
	Cell large and broad, epitheca rounded; antapicals usually equal or subequal, usually recurved. Subgenus *Euceratium*	21

2 (1).	Epitheca obovate: surface reticulate	*C. cephalotum*
	Epitheca ovate; hyaline	*C. gravidum*
3 (1).	Freshwater forms; usually 3 antapicals	*C. hirundinella*
	Salt-water forms	4
4 (3).	Body broader than long	*C. candelabrum*
	Body not broader than long	5
5 (4).	Epitheca tapering for 1/3 length or more	6
	Epitheca tapering for less than 1/3 length	8
6 (5).	Epitheca tapering for about 1/3 length	11
	Epitheca tapering to apex	7
7 (6).	Antapicals straight, tapering	*C. belone*
	Left antapical curved at tip	*C. incisum*
8 (5).	Cell pentagonal, linear markings obvious	9
	Cell pentagonal, linear markings not obvious	10
9 (8).	Cell equidimensional	*C. pentagonum*
	Cell longer than broad	*C. lineatum*
10 (8).	High apical horn, about 3 times body length	*C. pentagonum*
	High apical horn, more than 3 times body length	*C. setaceum*
11 (6).	Epitheca sides straight or concave: antapicals well developed	12
	Epitheca sides convex: antapicals small	13
12 (11).	Cell sculptured, antapicals spiny	*C. furca*
	Cell delicate, antapicals smooth	*C. kofoidii*
13 (11).	Apical long, no linear markings	*C. teres*
	Apical short, linear markings present	*C. minutum*
14 (1).	Apical sigmoid	15
	Apical curved to left at junction of body	16
15 (14).	Keel-like structure in epitheca; apical horn evident	*C. geniculatum*
	No keel-like structure in epitheca; horn continuous with epitheca	*C. falcatiforme*
16 (14).	Epitheca obviously swollen	*C. inflatum*
	Epitheca not obviously swollen	17
17 (16).	Right antapical absent or rudimentary	18
	Right antapical present	19
18 (17).	Small form (up to 500 μ long)	*C. fusus*
	Large form (up to 1280 μ long)	*C. extensum*
19 (17).	Large form (750-1280 μ long)	*C. extensum* var. *strictum*
	Small form (up to 300 μ long)	20
20 (19).	Apical horn obviously bent	*C. falcatum*
	Apical horn straight or slightly bent	*C. longirostrum*
21 (1).	Right antapical recurved and long, left short, directed rearward or sideways	*C. dens*
	Left and right antapicals equal or subequal; left antapical not directed rearward or sideways	22
22 (21).	Right antapical short, recurved	23
	Right and left antapicals equal or subequal, recurved	24
23 (22).	Right antapical diverging	*C. pulchellum* (*eupulchellum*)
	Right antapical following body contour	*C. schmidtii*
24 (22).	Base convex	25
	Base straight or slightly concave; antapicals directed rearwards and outwards	45
	Base straight or slightly convex; both antapicals directed backwards	47
	Base straight or slightly convex; one antapical directed outwards, the other backwards	*C. reflexum*

25(24). Apical horn with evident wings at base 26

Apical horn wingless or wings small 32

26(25). Wings serrate 27

Wings not serrate 29

27(26). Antapicals thickened but not winged .. .. .. *C. porrectum*

Antapicals thickened with serrate wings at base 28

28(27). Antapicals tapering .. .. .. *C. compressum*

Antapicals distended laterally, flattened .. .. .. *C. platycorne*

Antapicals ending in 5-7 "fingers" .. .. .. *C. ranipes*

29(26). Antapicals diverging .. .. .. *C. petersii*

Antapicals parallel to apical or converging 30

30(29). Epitheca humped .. .. .. *C. limulus*

Epitheca not humped 31

31(30). Epitheca tapering into straight apical horn; girdle incomplete . *C. azoricum*

Epitheca rounded, apical horn bent; girdle complete .. .. .. *C. arietinum*

32(25). Apical horn strongly curved 33

Apical horn strongly curved only at base 34

33(32). Right antapical close to and parallel to apical horn .. .. .. *C. axiale*

Right antapical evenly curved, ending almost at right angles to apical .. .. .. *C. arietinum*

34(32). Antapicals evenly curved 35

Antapicals more or less abruptly curved, then straight 40

Right antapical sigmoid 43

35(34). Epitheca low 36

Epitheca high 37

36(35). Left antapical shorter than right .. .. .. *C. humile*

Antapicals approximately equal .. .. .. *C. breve*

37(35). Right and left antapicals of equal length 38

Right antapical longer than left 39

38(37). Epitheca rounded; antapical parallel to apical .. .. .. *C. bucephalum*

Epitheca tapering into apical; subconical antapicals converging .. .. .. *C. symmetricum*

Epitheca slightly winged; apical usually short; antapicals long, forming a semicircle .. .. .. *C. lunula*

39(37). Girdle incomplete; base making sharp angle ($< 45°$) with long axis .. .. .. *C. euarcuatum*

Girdle usually complete; base making angle $> 45°$ with long axis .. .. .. *C. declinatum*

40(34). Left antapical sharply bent towards apical, then straight .. .. *C. longinum*

Left and right antapicals evenly curved, then straight 41

41(40). Base somewhat flat, continuous with antapicals *C. pulchellum* (*semipulchellum*

Base convex 42

42(41). Antapicals ending parallel with apical or diverging .. .. .. *C. tripos*

Right antapical bent at tip, often curled .. .. .. *C. karstenii*

43(34). Epitheca polygonal, coarsely reticulate .. .. .. *C. paradoxides*

Epitheca angular on right side with irregular linear markings .. *C. gibberum*

Epitheca rounded 44

44(43). Right antapical recurved close to and parallel with body, then turning parallel with margin of epitheca; girdle strongly angled ventrally .. .. *C. concilians*

Right antapical continuous with base, then gently twisted towards apical horn; girdle slightly angled ventrally .. .. .. *C. contortum*

45(24). Antapicals directed rearwards, then ventrally and at right angles to or parallel with apical horn .. .. .. *C. deflexum*

Antapicals coplanar with body in lateral view 46

Right antapical parallel to and almost colinear with apical, directed strongly backwards, then bending forwards or outward 57

46(45). Antapicals regularly recurved, then straight; body rounded .. *C. macroceros*

Antapicals directed sharply rearward, then forward and often wavy or bent again .. .. *C. macroceros* subsp. *gallicum*

47(24). Body strongly distorted; strong hexagonal markings .. .. .. *C. hexacanthum*

Body not strongly distorted; markings not hexagonal 48

48(47). Apical strongly bent towards right antapical, with which it is almost parallel 49

Apical not strongly bent 50

49(48). Horns winged and toothed; left antapical inordinately diverging . *C. longipes*

Horns not winged or toothed; left antapical at right angles to apical .. .. *C. arcticum*

50(48). Antapicals broadly U shaped .. .. *C. trichoceros*

Antapicals not broadly U shaped 51

51(50). Apical and antapicals exceedingly long and slender 52

Apical and antapicals stout 54

52(51). Apical and antapicals parallel or subparallel, not swollen at ends .. .. *C. longissimum*

Apical and antapicals parallel or subparallel, swollen at ends 53

Apical and antapicals inclined 54

53(52). Ends of antapicals clavate, sculptured .. .. .. *C. buceros* forma *claviger*

Ends of antapicals swollen, not sculptured .. .. .. *C. buceros* forme *molle*

54(52). Small forms, with short rather stout or long horns 55

Medium forms, horns stout, toothed .. .. *C. horridum*

Large forms, with very long horns slightly or not winged; toothed only at base 56

55(54). Antapicals equally inclined to apical, incurved at ends .. .. *C. buceros* forma *inclinatum*

Antapicals parallel, at right angles to apical . *C. buceros* forma *tenuissimum*

Antapicals rather stout, inclined .. .. *C. buceros* forma *tenue*, forma *denticulatum*, and forma *leptosomum*

56(54). Right antapical starting backwards at sharp angle, then rapidly bent forwards, outwards .. .. *C. massiliense*

Right antapical starting laterally, curving forwards or outwards, may be recurved backwards at tip .. .. *C. carriense*

57(45). Antapicals stout, base denticulate .. .. *C. vultur*

Antapicals not stout, base smooth .. .. *C. pavillardii*

Subgenus ARCHAECERATIUM Jörgensen

Archaeceratium Jörgensen, 1911.

Section *Poroceratium* Vanhöffen, 1899

CERATIUM CEPHALOTUM (Lemmermann) Jörgensen

Fig. 185

Ceratium cephalotum (Lemmermann) Jörgensen.
Ceratium cephalotum Jörgensen, 1911.
C. gravidum var. *cephalotum* Lemmermann, 1900.
C. gravidum var. *hydrocephala* Schröder, 1906.

Epitheca without apical horn, rounded, broad, and flat, obovate to reniform. Ring pore present. Hypotheca short; antapicals rather short, strong, not or slightly diverging, the left about twice as long as the right. Theca porulate.

Distribution.—Tropical, oceanic. Atlantic Ocean from 21°S. to 32°N. Indian Ocean (Karsten 1906), South of Reunion, between Ceylon and Sumatra; Pacific Ocean, Japan, west subequatorial stream, Solomon Is. (rare), east coast of Australia (rare) (Steemann Nielsen 1934). In the present survey, occurred off Trial Bay, N.S.W., and off Cowan Cowan, Moreton Bay, Queensland. Only found on east coast.

CERATIUM GRAVIDUM Gourret

Fig. 186*a-c*

Ceratium gravidum Gourret, 1883.
C. oviforme von Daday, 1888.
Poroceratium gravidum Vanhöffen, 1896.
C. gravidum var. *latum* Jörgensen, 1911.

Epitheca without apical horn, rounded, flat, ovate, broadest in upper $\frac{1}{3}$, broadening rapidly above transverse furrow. Hypotheca quadrilateral, base oblique or curved, antapicals thin-walled, left longer than to twice as long as right, diverging, right may be converging, both straight or bent. Theca hyaline.

Distribution.—Tropical oceanic. Atlantic Ocean from 27°S. to 48°N. Indian Ocean, Réunion to Sumatra; Pacific Ocean, Japan; south equatorial stream, Solomon Is. (rare), New Zealand (North I.), east Australia (Steemann Nielsen 1934), Port Jackson, N.S.W. (Whitelegge 1891). In the present survey occurred sparsely between Eden, N.S.W., and Point Danger, Queensland border, twice in Port Hacking, N.S.W., 2 miles from entrance in winter. The last occurrence is interesting since both Steemann Nielsen and Graham classified this as a shade species. Recorded in May-June, December-January. Also found in Southern Ocean at 2 stations south of Port Fairy with surface temperature of 13°C.

Subgenus BICERATIUM Vanhöffen

Biceratium Vanhöffen, 1897.

Section *Candelabra* Jörgensen, 1911

CERATIUM CANDELABRUM (Ehrenberg) Stein

Ceratium candelabrum (Ehr.) Stein, 1883.
Peridinium candelabrum Ehrenberg, 1859.
C. furca var. *depressa* Pouchet, 1883.
C. furca var. *contorta* Pouchet, 1883.
C. globatum Gourret, 1883.
C. dilatatum var. *parvum* Gourret, 1883.

Body broader than high. Epitheca obliquely conical, sharper, tapering into a long apical horn, which is straight or slightly bent; hypotheca very shallow, triangular. Antapicals short or long, thick or thin, straight or curved, diverging or parallel.

CERATIUM CANDELABRUM forma COMMUNE Böhm

Forma *commune* Böhm, 1931.

Body slightly compressed, conical, length equal to or slightly less than breadth.

CERATIUM CANDELABRUM forma CURVATULUM Jörgensen

Fig. 187*a*

Forma *curvatulum* Jörgensen, 1920.

Body slightly compressed, horns slender, apical horn bent to the right.

CERATIUM CANDELABRUM forma DEPRESSUM Pouchet

Fig. 187*b*

Forma *depressum* Pouchet, 1833 (as *C. furca*).
C. dilatatum Gourret, 1883.
C. depressum Gourret, 1883.
C. candelabrum var. *dilatatum* (Gourret) Jörgensen, 1911.
C. candelabrum var. *depressum* (Pouchet) Jörgensen, 1920.
C. candelabrum var. *algerense* Schiller, 1928.

Body strongly compressed, low, much broader than high, relatively and absolutely broader than the type form. Horns long, slender or strong, straight or bent.

Distribution.—All warm and temperate seas to 57°N. (Jörgensen 1911). Oceanic and tropical (Ostenfeld 1931). Pacific Ocean. Boeton Str., Celebes (Ostenfeld 1915), south equatorial stream, Solomon Is., New Zealand (North I.), east Australia (Steemann Nielsen), Port Jackson (Whitelegge), forma *commune* as *C. globatum*, and forma *depressum* as var. *dilatatum*. In the present investigation, only forma *curvatulum* and forma *depressum* have been found, except in the Great Barrier Reef region where forma *commune* was the only form seen, the form being rare. The species is moderately common on the east of Australia between Eden and Trial Bay, N.S.W., rare in east Tasmania, in the Solomon Is., New Britain, and New Ireland, in southern Australian waters from Albany to Israelite Bay, W.A., and south of Port Fairy, Vic.

Section *Cornuta* Jörgensen, 1911

CERATIUM HIRUNDINELLA (O. F. Müller) Bergh

Fig. 188

Ceratium hirundinella (O. F. Müller) Bergh, 1882.
Bursaria hirundinella O. F. Müller, 1773.
Ceratium macroceras Schrank, 1802.
C. tetraceras Schrank, 1802.
C. reticulatum Imhof, 1884.
C. longicorne Perty, 1849.
C. cumaonense Carter, 1871.
C. brevicorne Zacharias, 1905.
C. leptoceras Zacharias, 1905.
C. pumilum Zacharias, 1905.

Cell strongly flattened dorsoventrally, apical horn long and narrow, terminating abruptly. Hypotheca low and broad. Two or 3 hind horns, 1 antapical, 2 post-equatorial, all 3 different in length and direction. Theca surface varies. A highly variable form.

Type *gracile* (Bachmann, 1911)

A 4-horned type 60-75 by 140-200 μ. Apical and antapical horns almost in line.

Distribution.—Fresh water, north European and north Asia, rarer in North America. Recorded by Whitelegge from Port Jackson, N.S.W. One specimen found in this investigation in Port Hacking, possibly an aberrant form of *C. furca.*

Type *brachyceroides*

C. brachyceros von Daday.

Hypotheca usually shorter than epitheca. Right antapical directed towards centre line.

Distribution.—Swan River, W.A., March 1951.

Section *Furciformia* Jörgensen, 1911

CERATIUM FURCA (Ehrenberg) Claparède & Lachmann

Ceratium furca Claparède & Lachmann, 1859.
Peridinium furca Ehrenberg, 1833.
P. eugrammum Ehrenberg, 1859.
C. biceps Claparède & Lachmann, 1859.
Biceratium furca Vanhöffen, 1897.

A medium-sized species. Epitheca narrowing evenly, then drawn out into a short or long apical tube. Antapicals parallel or somewhat diverging, the left longer and stronger than the right, at most ½ as long again; both antapicals more or less pointed, frequently toothed.

CERATIUM FURCA var. BERGHII Lemmermann

Fig. 189*a*

Var. *berghii* (Jörgensen) Schiller, 1937.
Subsp. *berghii* Jörgensen, 1911.
C. furca var. *berghii* Lemmermann, 1900.

Epitheca rapidly tapering, apical horn usually longer than broad, often constricted to a point and bent. Antapicals usually somewhat diverging, the right relatively larger, usually longer than the transdiameter of the cell, seldom shorter, and about ½ as long as the left, both pointed; theca structure usually obvious (pores and ridges).

Distribution.—A widely distributed, plentiful temperate to cold-water form (Schiller 1937). In Australia, occurs from Port Jackson, N.S.W., to Storm Bay, Tas., and on the south coast from Albany, W.A., to Kangaroo I., S.A., and in Bass Strait. Is abundant at times in brackish water, e.g. upper Port Hacking, where it may be a major constituent of the phytoplankton.

CERATIUM FURCA var. EUGRAMMUM (Ehrenberg) Jörgensen

Fig. 189*b*, *c*

Ceratium furca var. *eugrammum* (Ehrenberg) Jörgensen, 1911.
P. eugrammum Ehrenberg, 1859.
now *C. eugrammum* Kofoid, 1907.
C. furca var. *medium* Gourret, 1883.
C. furca var. *pouchetii* Lemmermann, 1900.
C. furca var. *tertium* Gourret, 1883.

Smaller than the former variety. Epitheca usually tapers more slowly, apical angle smaller. Antapicals usually parallel, the right small, rarely ½ as long as the left, usually much shorter than the transdiameter, both horns pointed, seldom obviously spiny; apical horn almost always straight.

Distribution.—A warm-water form in all oceans, neritic in origin, usually sparse (Jörgensen 1911). Pacific, Boeton Str., Celebes (Ostenfeld 1915), Solomon Is., New Zealand (North I.), east Australia (commonest in the south) (Steemann Nielsen 1934), Port Jackson, N.S.W. (Whitelegge 1891). In eastern Australian waters moderately common between Eden, N.S.W., and Moreton Bay, Queensland, sometimes forming the main plankton element; rare in east Tasmanian waters and Storm Bay; rare in New Guinea and Solomon Is.; southern Australia from Albany to Kangaroo I., in Swan River, W.A., it is abundant at times. This species appears to take the place in Australian waters of *C. hirundinella* in European waters by appearing in brackish water, but is also common at times in waters of normal salinity as a neritic species. It was rarely found beyond the continental shelf, in which situation it is probably a guest.

CERATIUM BELONE Cleve

Ceratium bėlone Cleve, 1900.
C. pacificum Schröder, 1906.
C. furca longum Karsten, 1906.

A long slender form, with thickened apical and antapical horns.

Distribution.—Interoceanic warm-water form. Rare on east coast of Australia (Steemann Nielsen 1934).

CERATIUM INCISUM (Karsten) Jörgensen

Fig. 190

Ceratium incisum (Karsten) Jörgensen, 1911.
C. belone Okamura & Nishikawa, 1904; B. Schröder, 1906.
C. furca incisum Karsten, 1906.

Probably a form of *C. belone* Cleve, 1900 (Schiller 1937).

A moderately large species. Epitheca very narrow, lancet-shaped, gradually tapering from the transverse furrow to near the apex, where it becomes horn-shaped, bent slightly dorsally. Hypotheca parallel-sided, base angle large; antapicals very unlike, smooth, parallel, the left about twice as long and thick as the right, bent slightly dorsally and sideways, Theca walls strongly thickened on dorsal side; left horn thick, blunt pointed, the right thinner, sharper, straight.

Distribution.—A rare, warmer-water species. Rare in the Atlantic, west coast of Africa, Caribbean Sea, Ionian Sea, Indian Ocean, south of East Indies, Arabian Sea, Red Sea, South of Réunion; Pacific Ocean, in Japanese waters to 22°N., 140°E., and in the eastern Pacific to 10°S. (Graham 1942). Equatorial current and west Pacific (Steemann Nielsen 1934). Found in Port Hacking, N.S.W., in the winters of 1940 and 1950, obviously owing to oceanic influence, and east of Eden in August 1942 (new record for Australian waters).

Section *Pentagona* Jörgensen, 1911

CERATIUM PENTAGONUM Gourret

Fig. 191*a-f*

Ceratium pentagonum Gourret, 1883.
C. pentagonum var. *rectum* Gourret, 1883.
C. furca var. *pentagonum* Lemmermann, 1900.
C. furca var. *baltica* Schütt, 1895.
C. lineatum var. *longiseta* Ostenfeld & Schmidt, 1901.
C. lineatum var. *robusta* Cleve, 1900.
C. candelabroides Schimper & Vanhöffen, 1904.
C. subrobustum Steemann Nielsen, 1934.

A medium-sized species, transverse furrow somewhat below middle. Epitheca 3-cornered with almost straight contour lines at right angles. ending suddenly in a long, thin apical horn which is straight or slightly bent. In the large form (forma *robusta* Cleve) this horn is somewhat broad and winged at the base. Hypotheca short, trapezoidal with sides at first convex then concave, base usually oblique, making a shallow angle with transverse furrow. Antapicals short, the right usually less than $\frac{2}{3}$ left, both pointed, diverging slightly. Structure usually fragile, but there are (usually larger) forms which are richly covered with large pores and longitudinal ridges, and usually wings along the 3 horns. Such a form is forma *robustum* Cleve.

According to Jörgensen (1911), *C. lineatum* is a smaller, northern form.

The forms *robustum* Cleve (Fig. 191*a*), *subrobustum* Jörgensen, and *tenerum* (Fig. 191*c*) (Jörgensen) Schiller, occur on the Australian coast, but more common is a very large, strongly sculptured form with a short, stout apical horn, the body being much larger than that of any other *Ceratium* observed in Australian waters except *C. cephalotum* and *C. gravidum* (Fig. 191*d*). Smaller than this, but larger than normally recorded for forma *robustum* is the long-horned form found in Heard I. plankton (Fig. 191*e*), forma *robustum* of Peters.

Distribution.—Jörgensen (1911) recorded *C. pentagonum* as a warm-water species in the Atlantic, including the Mediterranean, to 45°S., in the Indian Ocean, and in the Pacific (Japan). Hardy (1936) recorded var. *setaceum* (? = *C. setaceum*) from South Georgia, and Hart (1936) also recorded this species from the Antarctic, north and south of the convergence (he recorded formae *grandis* and *robustum*, Steemann Nielsen (1934) recorded the species from the Solomon Is., North I. of New Zealand, and east Australia, while Whitelegge (1891) recorded it from Port Jackson, N.S.W.). In the present investigation the author has recorded it from the east and south coasts of Australia and from Heard I. The largest forms were found off the New South Wales coast and smaller *robustum* forms were found further south, in Bass Strait and in Heard I. and the Antarctic. This does not agree with Steemann Nielsen's statement that the largest forms occur in the coldest waters.

CERATIUM LINEATUM (Ehrenberg) Cleve
Fig. 192*a*, *b*

Ceratium lineatum Cleve, 1899.
Peridinium lineatum Ehrenberg, 1854.
C. furca var. *lineatum* Jörgensen, 1899.
C. setaceum robustum Peters, 1932.

Small species, body much longer than broad, girdle a little behind middle. Epitheca triangular with nearly straight sides, which usually make an angle of about 55° with each other. Apical horn clearly marked, tapering slightly, long. Hypotheca trapezoidal. Antapicals straight, more or less diverging to parallel, right $\frac{1}{3}$-$\frac{2}{3}$ length of left. Theca with conspicuous lines and pores. Closely related to *C. pentagonum*, of which it has been regarded as the cold-water representative in neritic situations.

Distribution.—Northern form of temperate and cold Atlantic, common in the European coast, especially in the North Sea and Norwegian Seas, also on the American side north of the Gulf Stream, probably also in northern Japan, north of the convergence. In this investigation occurs in Storm Bay, Tas., and in the Antarctic (B.A.N.Z.A.R.E.).

CERATIUM TERES Kofoid
Fig. 193

Ceratium teres Kofoid, 1907.
Ceratium lineatum var. *longiseta* Okamura, 1906 (1907).
C. teres var. *subturgidum* Jörgensen, 1920.

A small species closely related to *C. pentagonum*. This species usually has a long, thin apical horn but differs from *C. pentagonum* in the shape of the body and the very small right antapical. Epitheca elongated triangular from base of apical horn, with a slightly convex contour making an apical angle of 45-50°. Hypotheca rapidly narrowing, the left contour usually a little concave above. Base oblique. Antapicals sharply diverging, the right about $\frac{2}{3}$ length of left, both very finely toothed at the point.

Thecal wall usually hyaline and structureless, delicate on horns, pores very faintly marked, suture lines rarely evident.

There is also a more clearly sculptured form with short to very short apical horn, which shows large wings at the base. Body flat as in *C. pentagonum.* Transverse furrow well below the middle.

Distribution.—Fairly widely distributed, oceanic warm-water species, rarer than *C. pentagonum,* Atlantic, Azores, Gibraltar, Portugal, and west thereof. West coast of Africa (7-8°N.). Indian Ocean between Ceylon and Sumatra, south to 38°S., 77-79°E. Pacific Ocean, San Diego, Japan, south equatorial current, Solomon Is., North I. of New Zealand, east Australia. In this survey it was found on the east coast of Australia from Port Stephens, N.S.W., to Sandy Cape, Queensland, common in Port Hacking in winter; off New Guinea, north-west of New Britain, from 1 station off Albany, W.A., confirming the existence of tropical water off the SW. of Australia, and south of Port Fairy, Vic.

CERATIUM SETACEUM Jörgensen

Fig. 194*a, b*

Ceratium setaceum Jörgensen, 1911.
C. furca var. *baltica* Entz 1902?; Böhm, 1931.
?C. kofoidii Graham & Bronikowsky, 1944.

Similar to *C. kofoidii* but much longer, and very similar in dorsal view to *C. pentagonum.* The body is broader than *C. kofoidii,* hypotheca much more tapered antapically with sides at first convex, then concave. Antapicals rather stronger, apical horns long, pointed, sometimes very thin and long, with spiral scattered lines.

Distribution.—Very rare warm-water form found in the Azores and as far south as 27°S. in the Atlantic. Found by Steemann Nielsen (1934) at 1 station north of Samoa and 1 off the North I. of New Zealand, and from 2 stations, 1 off Peru and 1 between Guam and Japan by Graham and Bronikowsky (1944). In this study, was found between Trial Bay and Port Hacking, N.S.W.

CERATIUM KOFOIDII Jörgensen

Fig. 195

Ceratium kofoidii Jörgensen, 1911.
C. furca var. *baltica* Entz, 1902 partim.
C. bohmii Graham and Bronikowsky, 1944.

A small, fragile species, the smallest of the genus. Transverse furrow rather below the middle. Epitheca triangular with straight or slightly convex sides and a long, very thin apical horn, usually winged and somewhat broader at base. Hypotheca broader than long, slightly tapered with straight or slightly concave sides. Antapicals unequal, usually very thin, ending in a long fine point, somewhat diverging, may be finely toothed. The left at least twice as long as the right. Base contour somewhat oblique. Theca may be finely toothed or pored, but fragile.

Distribution.—A rare warm-water species, Atlantic, Azores to 10°S., Mediterranean, Indian Ocean (Valdivia Exped.), Gulf of Siam (*C. lineatum* Schmidt), Pacific Ocean, Formosa Strait, Japan, west coast of America, south equatorial stream, Solomon Is., and east Australia, inside the Great Barrier Reef (very rare, Steemann Nielsen 1934). In this investigation it appeared off southern New Guinea, in Moreton Bay, Queensland, rarely in Port Hacking, N.S.W., north of Trial Bay, N.S.W., where it was relatively numerous at times, usually accompanied by *C. teres.* In August 1952 it occurred off Eden, N.S.W.

CERATIUM MINUTUM Jörgensen

Fig. 196

Ceratium minutum Jörgensen, 1920.
C. eugrammum Kofoid, 1907.
non *P. eugrammum* Ehrenberg.

A small species of the Furciformia with rotund mid body and short horns. Mid body with convex margins and very convex dorsal face, hollow ventrally. Girdle somewhat anterior with prominent wings. Apical horn short. Antapicals very short, pointed, slightly or not divergent. Surface of theca with linear striae.

Distribution.—A temperate species recorded from the Atlantic (Jörgensen 1920; Lebour 1925; Peters 1932) and east Pacific (Kofoid 1907). Is rather rare from Babel I. to Fraser I. on east Australian coast and also on the southern and western coasts of Australia.

Subgenus AMPHICERATIUM (Vanhöffen) Gran

Section *Inflata* Jörgensen, 1911

CERATIUM GENICULATUM (Lemm.) Cleve

Fig. 197

Ceratium geniculatum (Lemm.) Cleve, 1901.
C. fusus var. *geniculatum* Lemmermann, 1900.
C. tricarinatum Kofoid, 1907.

Medium-sized species of characteristic habit. Epitheca in ventral view above girdle first narrowed, with convex sides, then somewhat swollen for a considerable way, constricted in the upper $\frac{1}{3}$ to a small, parallel-sided apical tube. Body triangular in section, then with 3 large longitudinal lobes, which in young forms are little developed and later can be easily seen. Left antapical very strong, bent twice, first to the right and ventrally, then to the left and dorsally, rather thick-walled. Right antapical clearly marked and relatively strong, narrow and pointed, at least 5 times shorter than left. Apical horn relatively short, about $\frac{1}{2}$ as long as the rest of the epitheca, deflected ventrally.

Distribution.—Rare warm-water form. Atlantic, 26°N. to 20°S.; Indian Ocean, East Africa, Ceylon to northern tip of Sumatra and off Sumatra (Valdivia Exped.); Pacific Ocean (10-19°S., Kofoid 1907), very rare in equatorial current (Steemann Nielsen 1934). One station off Crowdy Head, N.S.W., on 26.v.1942 (new record).

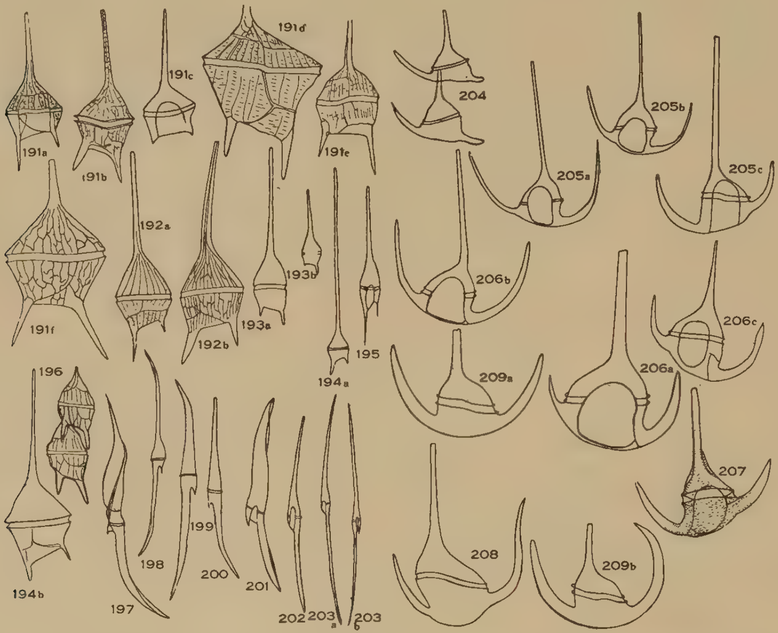


Fig. 191.—*a, b, Ceratium pentagonum* Gourret forma *robustum* Cleve, 1900. *a*, Eden; *b*, Antarctic (B.A.N.Z.A.R.E.); *c, C. pentagonum* forma *tenerum* (Jörg.) Schiller, 1937; Port Hacking; *d, C. pentagonum*, large form from east Australian waters; *e, C. pentagonum*, Antarctic form, Heard I.; *f, C. pentagonum*, Antarctic form. (B.A.N.Z.A.R.E.). Fig. 192.—*C. lineatum* (Ehrenberg) Cleve, 1899. *a*, Storm Bay, Tasmania, *b*, Antarctic (B.A.N.Z.A.R.E.). Fig. 193.—*C. teres* Kofoid, 1907. *a*, Cowan Cowan, Moreton Bay; *b*, Port Hacking. Fig. 194.—*C. setaceum* Jörgensen, 1911. *a*, Montague I.; *b*, Trial Bay. Fig. 195.—*C. kofoidii* Jörgensen, 1911. New Guinea. Fig. 196.—*C. minutum* Jörgensen, 1920. Port Hacking. Fig. 197.—*C. geniculatum* (Lemmermann) Cleve, 1901. Jibbon Cape. Fig. 198.—*C. inflatum* (Kofoid) Jörgensen, 1911. Jibbon Cape. Fig. 199.—*C. longirostrum* Gourret, 1883. Trial Bay. Fig. 200.—*C. falcatum* (Kofoid) Jörgensen, 1920. Jibbon Cape. Fig. 201.—*C. falcatiforme* Jörgensen, 1920. *a*, Trial Bay; *b*, Port Hacking. Fig. 202.—*C. fusus* (Ehrenberg) Dujardin, 1841. Port Hacking. Fig. 203.—*a, C. extensum* (Gourret) Cleve, 1901. Jibbon Cape; *b, C. extensum* forma *strictum* (Okamura & Nishikawa) Steemann Nielsen, 1934. Lord Howe I. Fig. 204.—*C. dens* Ostenfeld & Schmidt, 1901. Montague I. Fig. 205.—*a, C. tripos* var. *atlanticum* Ostenfeld, 1903. Bass Strait; *b, C. tripos* forma *balticum* Schütt, 1892. Port Phillip; *c, C. tripos* forma *tripodioides* (Jörgensen) Paulsen, 1930. Trial Bay. Fig. 206.—*a, C. pulchellum* (*eupulchellum*). Jibbon Cape; *b, c, C. pulchellum* forma *semipulchellum* Jörgensen, 1920. *b*, Jibbon Cape; *c*, Bass Strait. Fig. 207.—*C. porrectum* Karsten, 1907. Fig. 208.—*C. humile* Jörgensen, 1911. Fig. 209.—*a, b, C. breve* (Ostenfeld & Schmidt) Schröder, 1906.

Section *Fusiformia* Jörgensen, 1911

CERATIUM INFLATUM (Kofoid) Jörgensen

Fig. 198

Ceratium inflatum (Kofoid) Jörgensen, 1911.
C. fusus var. *concavum* Gourret, 1883.
C. pennatum forma *inflata* Kofoid, 1907.
non *C. pennatum* forma *propria* Kofoid, 1907 = *C. longirostrum* Gourret.

Large species, epitheca moderately broad, constricted sharply into a long apical horn which is cylindrical at first, then sharply tapering to a point, and more or less bent dorsally. Left antapical very long, symmetrical, strongly bent dorsally, sharply tapering to a point, both apical and antapical strongly thickened dorsally near tip. Right antapical very small but always apparent. The author agrees with Peters that *C. longirostrum*, *C. falcatum*, and *C. falcatiforme* are possibly clones of this species. Graham and Bronikowsky also consider this to be a distinct possibility.

Distribution.—Warm-water species, widely distributed but usually sparse. Atlantic Ocean, Caribbean, Florida current to 52°N., south and east to 20°S.; Mediterranean; Indian Ocean, Red Sea, Ceylon to Sumatra, South China Sea, East Indies; Pacific, Japan, California, Solomons, New Zealand (North I.), east Australia (very rare, Steemann Nielsen 1934). In this investigation at 1 station off Port Stephens, N.S.W., 1.i.1941.

CERATIUM LONGIROSTRUM Gourret

Fig. 199

Ceratium longirostrum Gourret, 1883.
C. pennatum forma *propria* Kofoid, 1907.
C. pennatum var. *scapiforme* Jörgensen, 1911.
non *C. scapiforme* Kofoid, 1907.

Medium to small species. Epitheca very long and narrow, gradually (sometimes imperceptibly) tapering into apical horn, bent dorsally. Hypotheca tapering slightly, rather longer than broad. Left antapical long, more or less strongly bent to the left and dorsally, concave side strongly thickened. A similar but lesser thickening occurs in the corresponding part of apical horn. Right antapical evident but small, narrow, thin, bluntly pointed.

Distribution.—Warm-water species, rare. Atlantic, near Azores, Mediterranean, Indian Ocean, Red Sea, Arabian Sea, Indian Ocean from 37°S. to 7°N., Pacific Ocean, Japan, East Pacific, North I. of New Zealand, and east Australian coast (Steemann Nielsen 1934). Found in this investigation at a few stations north of Port Jackson, N.S.W.

CERATIUM FALCATUM (Kofoid) Jörgensen

Fig. 200

Ceratium falcatiforme Jörgensen, 1920.
C. pennatum forma *falcata* Kofoid, 1907.
C. pennatum var. *falcatum* Jörgensen, 1911.

Characterized by the slightly bent or almost straight apical horn, which is usually longer than the left antapical, which is sharply bent to the left. Epitheca at first almost cylindrical, then gradually tapering into the apical horn.

Distribution.—Interoceanic warm-water form. Widely distributed in the Mediterranean. Very rare in tropical Pacific, North I. of New Zealand, and east Australia (Steemann Nielsen 1934). Not infrequent in Bantry Bay, Sydney Harbour, in October 1949; Port Hacking, N.S.W.; Southern Ocean south of Port Fairy, Vic.

CERATIUM FALCATIFORME Jörgensen
Fig. 201*a*, *b*

Ceratium falcatiforme Jörgensen, 1920.
Ceratium falcatiforme Peters, 1932.
C. scapiforme Kofoid, 1907.

Similar to *C. longirostrum* and *C. falcatum* but smaller. Epitheca like *C. longirostrum,* but apical horn more curved, more gradual transition from body to horn. Antapical is less abruptly curved than with *C. falcatum.*

Distribution.—Interoceanic warm-water species, Mediterranean, Atlantic, tropical Pacific, North I. of New Zealand, and east Australia (very rare, Steemann Nielsen 1934). One station off Point Danger and off Port Hacking, N.S.W., in this investigation.

CERATIUM FUSUS (Ehrenberg) Dujardin
Fig. 202

Ceratium fusus (Ehrenberg) Dujardin, 1841.
Peridinium fusus Ehrenberg, 1833.
P. seta Ehrenberg, 1859.
C. fusus var. *inaequalis* Schröder, 1900.
C. fusus var. *acus* von Daday, 1886.
Cercaria Michaelis, 1830.
Amphiceratium fusus Vanhöffen, 1899.
C. pellucidum Gourret, 1883.
C. berghii Gourret, 1883.

Medium or small species. Epitheca long, gradually tapering to a cylindrical or gently tapering apical horn usually slightly bent dorsally or almost straight. Hypotheca tapering, longer than broad. Left antapical long, usually curved evenly and more or less strongly, rarely almost straight, usually rough. Right antapical rudimentary or absent. Sometimes forming a small point. Variable species.

Two varieties (or better, forms) can be distinguished.

CERATIUM FUSUS var. SCHUTTII Lemmermann

Var. *schüttii* Lemmermann, 1900.
C. fusus Schütt, 1895.

Epitheca at first widened above girdle, then tapering. Hypotheca relatively longer than the epitheca.

Distribution.—Numerous in the mixed or cool areas of the Atlantic.

CERATIUM FUSUS var. SETA (Ehrenberg) Jörgensen

Var. *seta* (Ehrenberg) Jörgensen, 1911.
P. seta Ehrenberg, 1859.
C. seta Kent, 1852; Kofoid, 1908.

Smaller and more delicate. Horns thinner than in the above variety. Epitheca usually shorter than hypotheca, rarely equally long or longer. Horns smooth, slightly curved or almost straight. Right horn usually absent.

Distribution.—Warm water in all oceans. Recorded by Ostenfeld (1915) from Boeton Strait, Celebes; by Steemann Nielsen (1934) in Solomon Is., New Zealand, and east Australia. Whitelegge (1891) recorded *C. fusus* from Port Jackson, N.S.W. In this investigation, *C. fusus* var. *seta* occurs off Cape Inscription and in Swan River, W.A., on the south and east coasts of Australia, and is a common estuarine form in the Sydney region, at times being a major phytoplankton constituent.

CERATIUM EXTENSUM (Gourret) Cleve
Fig. 203*a*

Ceratium extensum (Gourret) Cleve, 1901.
C. fusus var. *extensum* Gourret, 1883.

A very long species. Epitheca long and narrow, continuous with a long, straight, narrow apical horn. Left antapical unusually long, diverted slightly dorsally, but straight. Right antapical absent. Epitheca usually shorter than hypotheca.

Distribution.—Tropical, oceanic, sparsely distributed (Jörgensen 1911). Recorded from Atlantic 28°S. to 50°N., Mediterranean, Indian Ocean, 44°S. to Red Sea and Sunda Strait, Celebes, Pacific Ocean, Japan, and Formosa. South China Sea south equatorial current, Solomon Is., New Zealand (North I.), east Australia (Steemann Nielsen 1934). Moderately frequent between St. Helen's and Moreton Bay, Queensland, on the east coast of Australia; in the Tasman Sea, and off Lord Howe I. Rather rare in Western Australian waters. Not found in southern waters except at eastern extremity of west wind drift just west of Bass Strait.

CERATIUM EXTENSUM forma STRICTUM (Okamura & Nishikawa) Steemann Nielsen
Fig. 203*b*

Ceratium extensum forma *strictum* (Okamura & Nishikawa) Steemann Nielsen, 1934.
C. strictum, Kofoid, 1907; Jörgensen, 1911, 1920; Forti, 1922; Paulsen, 1930.
C. fusus var. *stricta* Okamura & Nishikawa, 1904.

?*C. furca* var. *mediterraneum* Gourret, 1883.
C. biceps Kofoid, 1908.
? Claparède & Lachmann, 1858.

Differs from the proper form in having the right antapical developed —thin and sharp. Jörgensen (1911) considered *C. extensum* may be a regenerating form of the variety.

Distribution.—Generally as for *C. extensum.* In this investigation was moderately frequent between Montague I. and Moreton Bay and in New Guinea on the east coast, and in the Tasman Sea. Occurred at 1 station in Western Australia, not in southern waters.

Subgenus EUCERATIUM (Gran) Ostenfeld, 1901

Section *Dens* Jörgensen, 1911

CERATIUM DENS Ostenfeld & Schmidt

Fig. 204

Ceratium dens Ostenfeld & Schmidt, 1901.
C. dens var. *reflexa* Schmidt, 1901.

Rather large, robust species; body rather broader than long. Epitheca low, about ½ as long as broad. Apical horn strong, winged, cylindrical, broader at base, and except in the rear member of a chain, rather long, usually longer than the right antapical. Hypotheca low, about twice as broad as long with a regularly oblique basal contour. Left antapical remarkably short, only ⅔ transdiameter, directed obliquely to the left. Straight or slightly bent with a short, closed, blunt point. Right antapical continuous with base bent forward, diverging from apical horn, long, somewhat thinner than both other horns. Theca structure very marked: knobs, curved lines, and heavy, evident pores.

Distribution.—Rare, warm-water form; only from tropical Indian Ocean and its offshoots—Red Sea, Arabian Sea, Gulf of Siam, Banda Strait, Boeton Strait, east coast of Malacca, and in the Pacific Ocean in 2 samples off NE. Australia, 1 inside the Great Barrier Reef and 1 in Torres Strait (Steemann Nielsen 1934), eastern Pacific, 1 station (Pavillard 1935), and Malaya (Bohm 1931). This is regarded by Steemann Nielsen as a guest in the Pacific. However, the author has found it, moderately numerous, in a few samples from as far south as Montague I., N.S.W., and as far east as New Ireland and the Solomon Is., as well as in the Timor Sea. This distribution suggests that there is, at least at times, a strong flow of water from west to east through Torres Strait, sufficient to influence the plankton flora of the south-west Pacific along most of the east coast of Australia. *Ceratium dens* is therefore an important indicator species.

Section *Tripos* Ostenfeld, 1903

CERATIUM TRIPOS (O. F. Müller) Nitzsch

Ceratium tripos (O. F. Müller) Nitzsch, 1817.
Cercaria tripos O. F. Müller, 1781.

Peridinium tripos Ehrenberg, 1833.
Ceratium arcuatum Vanhöffen, 1897.
C. neglectum Ostenfeld, 1903.
C. tripos, pulchellum forma *tripodioides* Jörgensen, 1920.
C. tripodioides (Jörgensen) Steemann Nielsen, 1934.

Moderately large species; body about as broad as long, epitheca rather low, sometimes twice as broad as long, left contour slightly convex, right strongly convex. Hypotheca as long as epitheca or longer, left side more or less concave. All horns strong, apical broader below, larger than the others, right antapical usually markedly less developed than left. Antapicals diverging from one another and from apical horn, the right diverging least. Sometimes the right and left antapicals are parallel with the apical and rarely converging. Theca structure very strong, richly decorated with anastomosing lines, and ridged or toothed ribs.

Schiller (1937) recognized 1 variety (var. *atlanticum*) and 4 forms, forma *tripodioides*, forma *ponticum*, forma *balticum*, and forma *subsalsum*. *Ceratium tripos* is a highly variable form and intergrades have been found by the author in Victorian and Tasmanian waters between this species and *C. pulchellum* forma *semipulchellum*, which Graham and Bronikowsky (1944) considered a subspecies of *C. tripos*. Jörgensen (1920) created forma *tripodioides* as a form of the latter, Steemann Nielsen raised this form to a species, while Schiller followed Paulsen (1930) in transferring it to *C. tripos*. This shows the difficulty of separating the 2 species (if species they are) and of adequately defining *C. tripos*.

CERATIUM TRIPOS var. ATLANTICUM Ostenfeld
Fig. 205*a*

Ceratium tripos var. *atlanticum* Ostenfeld, 1903.

Antapicals usually of the same size, similarly bent, more or less diverging. Right antapical may be longer than left. Contour of these convex.

Distribution.—This is the oceanic North Atlantic variety, which is also abundant in other cool-temperate seas and tropical waters. It was recorded by Steemann Nielsen from New Zealand and is common in eastern Australian waters, while Hardy (1935) recorded it from South Georgia and Hart (1934) from the sub-Antarctic. This variety is the usual one met with on the east coast of Australia. In Port Phillip, Vic., and Bass Strait it occurs with forma *balticum* (Fig. 205*b*) and *C. pulchellum* forma *semipulchellum*.

CERATIUM TRIPOS forma TRIPODIOIDES (Jörgensen) Paulsen
Fig. 205*c*

Ceratium tripos forma *tripodioides* (Jörgensen) Paulsen, 1930.
C. pulchellum forma *tripodioides* Jörgensen, 1920.
C. tripodioides Steemann Nielsen, 1934.

This form grades into var. *atlanticum,* from which it differs slightly in the angle between girdle and base (t) and in the rounded base contour. It was recorded by Steemann Nielsen from the Solomon Is. and 1 station in east Australia. The author did not separate it from *C. tripos* var. *atlanticum,* regarding it as an intergrade with *C. pulchellum.*

CERATIUM TRIPOS forma BALTICUM Schütt

Fig. 205*b*

C. tripos forma *balticum* Schütt, 1892.

Antapicals unlike, diverging, the right smaller, at most as long as the body, more or less sharply bent at base. Left horn longer and stronger, usually regularly curved.

Distribution.—A winter-spring form in the northern Atlantic seas. Found by the writer in Storm Bay, Tas., and Port Phillip, Vic., as a usual constituent of the plankton.

CERATIUM PULCHELLUM B. Schröder

Fig. 206*a*

Ceratium pulchellum B. Schröder, 1906.

C. tripos var. *gracilis* B. Schröder, 1900; Ostenfeld & Schmidt, 1901; non Gourret, 1883.

C. pulchellum forma *postico-juvenile* Jörgensen, 1911; Forte, 1922.

C. tripos Peters, 1932 partim.

C. tripos semipulchellum Peters, 1932.

incl. *C. pulchellum* forma *eupulchellum* Jörgensen, 1920.

Medium-sized species. Epitheca rather high, about $\frac{3}{4}$ as long as broad, with convex but very steep left and very convex right side. Apical horn very long and strong. Cylindrical to the tip, little or no broader below, sometimes a little wider in the middle than at the ends. Hypotheca with slightly concave or straight and slightly oblique left side. Base convex, continuous with left antapical, while the right is clearly attached. Antapicals rather short, a little stronger than the apical horn, the left regularly curved, somewhat diverging or parallel to the apical horn, the right less strongly developed. May be equal in length or much shorter than left. Theca structure usually smooth and indistinct, but may have clear pores, and girdle strongly marked.

Distribution.—A warm-water form in all oceans. Stenohaline. Recorded from the Solomon Is., North I. of New Zealand, and eastern Australia by Steemann Nielsen (1934). Also observed by the author on the east coast of Australia, and in Storm Bay, Tas.

CERATIUM PULCHELLUM forma SEMIPULCHELLUM Jörgensen

Fig. 206*b, c*

Ceratium pulchellum forma *semipulchellum* Jörgensen, 1920.

C. tripos pulchellum Peters, 1932.

non *C. tripos semipulchellum* Peters, 1932 = *eupulchellum.*

C. semipulchellum Steemann Nielsen, 1934.
C. pulchellum Schröder, Forti, 1922

Differs from the type in a somewhat larger transdiameter and somewhat longer antapicals.

Distribution.—Very widely distributed warm-water form. Atlantic, from south tip of Africa to Cape Hatteras. Indian Ocean from southern tip of Madagascar to Sunda I., Pacific Ocean, Japan, equatorial current (western portion), Solomon Is., east Australia. The author has found this form frequent, usually with *C. tripos* in Storm Bay, Tas.

CERATIUM PORRECTUM Karsten

Fig. 207

Ceratium porrectum Karsten, 1907.
?C. divaricatum Kofoid, 1908.

Robust, medium-sized species, related to *C. tripos* and *C. breve.* Body appearance similar to that of *C. pulchellum* but broader. Left contour of epitheca clearly to strongly convex, less steep than with *C. pulchellum.* Apical horn strongly widened at base, sometimes in old individuals has large toothed wings, tip of horn rather narrow. Antapicals equally bent, usually rather short (about as long as body), diverging, sometimes long and parallel, rarely slightly converging, the right somewhat shorter and a little narrower than the left, very rarely equally long. Theca structure strong, large lines and pores, very thick-walled, sometimes with strong wings on the concave side of the antapicals. Graham and Bronikowsky (1944) considered this a form of *C. arietinum.*

Distribution.—Recorded from Seychelles by Karsten (1907) and de Sousa e Silva (1949) off Portugal. The author has found this species in Storm Bay and Port Arthur, Tas., and off Port Hacking, N.S.W.

CERATIUM HUMILE Jörgensen

Fig. 208

Ceratium humile Jörgensen, 1911.

Rather large, short-horned species. Epitheca unusually low. Hypotheca twice as long, base contour convex, may be strongly convex and knobbed. Apical horn almost cylindrical, a little broader in lower part, at times very short, rarely twice as long as body. Left antapical rather short, often directed a little forward, regularly and symmetrically curved, diverging. Right antapical obviously longer, directed somewhat forward at base, slightly curved, converging slightly. Theca strongly built in old forms with lines and knobs. Resembles *C. tripos, C. breve, C. euarcuatum,* and *C. karstenii.*

Distribution.—Rare warm-water species. Recorded from Atlantic by Graham and Bronikowsky (1944) and in Pacific, east of Japan, Solomon Is., and east Australia. Not in equatorial current along the coast of New South Wales, New Caledonia and Fiji (Steemann Nielsen 1934). Recorded by the author from Storm Bay, Tas., in October 1950.

CERATIUM BREVE (Ostenfeld & Schmidt) Schröder

Fig. 209*a*, *b*

Ceratium breve (Ostenfeld & Schmidt) Schröder, 1906.
Ceratium tripos var. *brevis* Ostenfeld and Schmidt, 1901.
Ceratium tripos azoricum Karsten, 1906 partim.
Ceratium breve var. *curvulum* and var. *parallelum* (Schmidt) Jörgensen, 1911.
Ceratium tripos var. *parallela* Schmidt, 1901.

Medium-sized short-horned species. Epitheca more than ½ as long as broad, left contour steep, right strongly and broadly convex. Apical horn short to 1½ times as long as body. Hypotheca usually clearly longer than epitheca or equally long with evenly convex base contour or strongly swollen in the middle, merging into both antapicals, which are unusually strong, left unusually straight, parallel with the apical horn, bent sharply at base and then straight, more or less converging. Theca structure usually clear; lines and large pores, low ridges along entire apical horn.

Distribution.—Rather rare tropical species. Atlantic, west coast of Africa, between Cuba and Haiti; Indian Ocean, 25°S., 50°E. to Red and Arabian Seas, Boeton Strait, Celebes (Ostenfeld 1915); Pacific; Panama area, Solomon Is., south equatorial current, neritic stations inside the Great Barrier Reef, east Australian current, rare south of Brisbane, not in New Zealand waters (Steemann Nielsen 1934). The author has found this species from Thursday I., and from Moreton Bay, Queensland, to Montague I., N.S.W., on the east coast of Australia. It is relatively common and at times numerous.

CERATIUM BUCEPHALUM (Cleve) Cleve

Fig. 210*a-c*

Ceratium bucephalum (Cleve) Cleve, 1901.
C. tripos var. *bucephalum* Cleve, 1897.
C. tripos var. *berghii* Lemmermann, 1900.
C. arcuatum Vanhöffen, 1897, partim: Jörgensen, 1899.
C. bucephalum var. *heterocamptum* Jörgensen, 1899, 1905.
C. heterocamptum Paulsen, 1908, vix Ostenfeld & Schmidt, 1901.

A rather small species. Body longer than broad. Apical horn rather long, straight or somewhat bent at base. Basal contour convex, continuous with antapicals, which arise transversely to body, strong, of equal size or the right a little smaller, curvature regular, then at points strongly converging and antapicals not reaching tip of apical. Wings along apical rare. Chromatophores numerous, plate-like in cell, banded in horns.

Distribution.—Temperate to cool water. Atlantic Portugal (de Sousa e Silva 1949), rare Plymouth and North Atlantic, North Sea, Florida Stream, Pacific, tropical water, and Japan. In this investigation was found in Storm Bay, Tas., and Port Hacking, N.S.W. It is also characteristic of Torres Strait and the Barrier Reef.

CERATIUM KARSTENII Pavillard

Fig. 211*a*, *b*

Ceratium karstenii Pavillard, 1907.
C. arcuatum (*tripos* var.) Cleve, 1900.
C. tripos var. *arcuata* Ostenfeld & Schmidt, 1903. non Gourret.
C. tripos var. *macroceros* forma *inflexa* Gourret, Schröder, 1900.
C. arcuatum Cleve, 1903. Jörgensen, 1920; Böhm, 1931; Karsten, 1906.
C. tripos lunula Karsten, 1906.
C. schrankii Kofoid, 1907.
C. tripos schrankii Karsten, 1907.
C. lunula var. *robusta* Karsten, 1907 partim.

A large robust species, epitheca: right contour strongly convex, longer than the slightly convex left. Apical horn bent at base, more or less inclined to left. Right antapical long and then usually bent towards apical at point, more rarely twisted. Many individuals, however, do not show this specific character. There are many transition forms. Left antapical shorter, often evenly curved, at most about twice as long as body, sometimes also bent at tip. Both horns slender distally, soft, and often without direction.

Distribution.—Plentiful in all oceans and offshoots. Atlantic, from southern tip of Africa to 37°N. on American side and 50°N. with Gulf Stream; Mediterranean; Indian Ocean, 36°S. to Red Sea and Sumatra; Pacific Ocean, East Indies, Formosa, south equatorial current, Solomons, North I. of New Zealand, east Australia. Occurs from Eden, N.S.W., to Fraser I., Queensland, and probably further north; New Ireland; Cape Inscription, W.A.

CERATIUM CONTORTUM (Gourret) Cleve

Fig. 212*a-c*

Ceratium contortum (Gourret) Cleve, 1900.
C. gibberum var. *contortum* Gourret, 1883.
C. subcontortum B. Schröder, 1906.
C. saltans B. Schröder, 1906.
C. contortum var. *saltans* Jörgensen, 1911.

Large species resembling *C. karstenii* and *C. longinum*. Epitheca oblique on right, right contour strongly convex. Apical horn clearly bent to the left and twisted, often almost S-shaped. Base contour convex, more or less swollen. Antapicals more or less unequal, the right longer (seldom equal to or shorter) than the left. The latter like that of *C. karstenii* in form and more or less parallel to apical horn at end. The right is twisted dorsally or ventrally and then towards the apical horn.

CERATIUM CONTORTUM forma SUBCONTORTUM (Schröder) Steemann Nielsen

Fig. 212*d*

Ceratium contortum forma *subcontortum* (Schröder) Steemann Nielsen, 1934.

Right antapical evenly curved.

Distribution.—Warm-water oceanic species. Frequent in all warm parts of Atlantic, rare in Mediterranean, Indian Ocean, Red Sea, and Zanzibar to Sunda I., 25°S. to 12°S., South China Sea, Gulf of Siam, east Malacca, Banka Strait, Pacific, Japan, south equatorial current, Solomon Is., east Australia (Steemann Nielsen 1934). Found in this investigation off Trial Bay and Sandy Cape on the east coast of Australia.

CERATIUM CONCILIANS Jörgensen

Fig. 213

Ceratium concilians Jörgensen, 1920.
non *C. contortum* Cleve, 1900.
C. tripos var. *contortum* Gourret, 1883.
C. tripos gracilis Entz, 1902.
C. gibberum forma *sinistrum* Jörgensen, 1911 partim.

Very like *C. gibberum,* but smaller; body not humped and basal contour more or less swollen to the left. Theca smooth, without the strong ribs and reticulation characteristic of *C. gibberum.* Apical horn bent, convex to left dorsally. Right antapical continuous with base, bent towards dorsal side of body, the distal end often bent again in the direction of the apical horn. Transitions to *C. gibberum* occur.

Distribution.—Interoceanic warm-water surface form, Mediterranean. Recorded by Steemann Nielsen from Solomon Is., south equatorial current, North I. of New Zealand, and south-east Australia. The author has recorded it from Trial Bay, Port Hacking, and Eden, N.S.W.; east of Tasmania (B.A.N.Z.A.R.E.); and west wind drift south of Port Fairy, Vic.

CERATIUM GIBBERUM Gourret

Fig. 214*a, b*

Ceratium gibberum Gourret, 1883.
C. tripos var. *megaceras* Pouchet, 1883.
C. tripos var. *curvicornis* von Daday, 1888.
C. concilians forma *dispar* (Pouchet) Böhm, 1931.

Body thick, rather flattened, epitheca low, angle of side contour blunt in dorsoventral plane, left side almost straight, right straight to strongly convex, humped. Apical horn bent to the left at base, then almost straight, strong with wings often transversely ridged. Hypotheca longer than epitheca with very oblique left side contour. Basal contour strongly convex, more or less bulged. Left antapical strong, evenly bent; right variable, directed from base sharply forward and ventrally then dorsally, often in a very variable manner. Theca wall strongly sculptured with ridges and pores.

CERATIUM GIBBERUM forma SUBAEQUALE Jörgensen

Fig. 214*c*

Ceratium gibberum forma *subaequale* Jörgensen, 1920.

Distribution.—Widely distributed warm-water form. Atlantic, 29°S. to 27°N., and with Gulf Stream to 45°N., Mediterranean, Indian Ocean, Red Sea, Gulf of Aden, Arabian Sea, east coast of Africa to North Sumatra, Gulf of Siam, Boeton Strait, Pacific, Japan, equatorial current, Solomon Is., east Australia (central portion), i.e. in all oceans with temperature above 20°C. The author records it from Eden, N.S.W., north on east coast of Australia, and from New Ireland.

CERATIUM LUNULA Schimper

Fig. 215*a*, *b*

Ceratium lunula Schimper, 1900.

C. lunula Schimper forma *megaceros* and forma *brachyceros* Jörgensen, 1911.

Epitheca almost triangular, rather oblique, with almost straight to faintly convex sides. Hypotheca shorter than epitheca to equally long with very faintly convex base. Apical horn of 1st cell of chain very long and strong, almost straight or slightly bent, of the other cells (and often of individuals) very short, the antapicals very long, more or less diverging or parallel at the ends, evenly curved from tip to tip through the base. In chains, single members may not be in the same plane.

Distribution.—Rare, interoceanic warm-water form. Occurs at times on the east coast of Australia from Eden, N.S.W., to Wide Bay, Queensland, and probably further north. More characteristic of the Western Australian flora from Cape Inscription to Israelite Bay, at the western side of the Great Australian Bight, and south of Port Fairy, Vic. Steemann Nielsen recorded this species from the Pacific, south equatorial current only. Recorded by Karsten from the Indian Ocean. Its occurrence in east Australian waters may indicate Indian Ocean water movement through Torres Strait, although the "Dana" tows in the south-west Pacific were too few for the absence of this species therefrom to rule out its movement south-west from the equatorial current.

CERATIUM SCHMIDTII Jörgensen

Fig. 216*a*, *b*

Ceratium schmidtii Jörgensen, 1911.

C. curvicorne Schmidt, 1901.

Large-celled form with short antapicals. Epitheca very high. Hypotheca longer than epitheca. Base convex, usually continuous with both antapicals. Apical horn long, slightly bent to left at base and widened with short, high wings. Antapicals very broad at base, sharply bent forward, shorter than body, strongly directed ventrally, the right again bent dorsally at tip. Like *C. gibberum*, from which it differs in the regular body contour, the very short large-based horns, and the wide, slightly curved base contour. Graham and Bronikowsky (1944) considered this probably a form of *C. breve* but this seems doubtful.

Distribution.—Rare warm-water form in the Indian and Pacific Oceans, South China Sea, Boeton Strait, Malacca, Gulf of Siam; not recorded by Steemann Nielsen (1934), except from the Panama zone. One example found from New Guinea waters 31.i.1950 in this investigation.

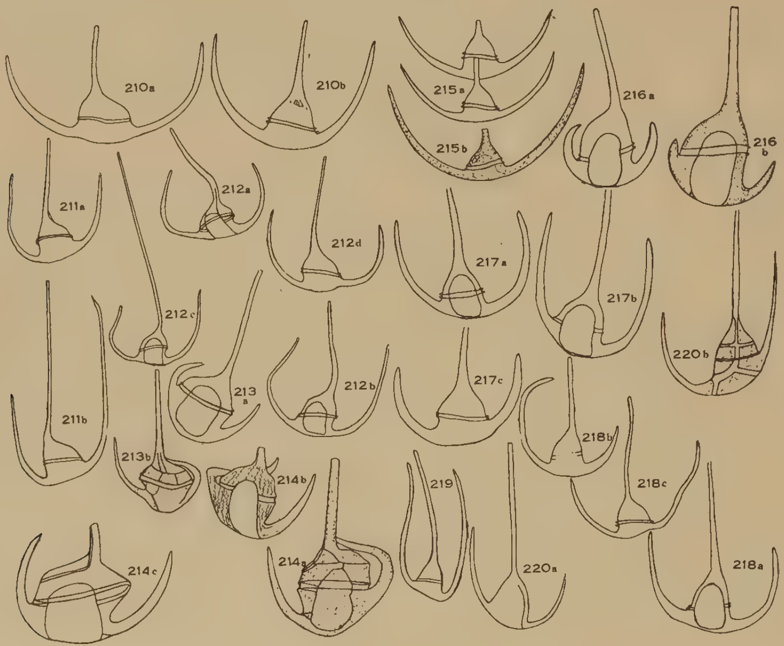


Fig. 210.—*a-c*, *Ceratium bucephalum* (Cleve) Cleve, 1901. *a*, Storm Bay; *b*, *c*, east Tasmania. Fig. 211.—*a*, *b*, *C. karstenii* Pavillard, 1907. *a*, Trial Bay; *b*, Port Stephens. Fig. 212.—*a-c*, *C. contortum* (Gourret) Cleve, 1900. *a*, Cape Moreton; *b*, *c*, Jibbon Cape; *d*, *C. contortum* forma *subcontortum* (Schröder) Steemann Nielsen, 1934. Montague I. Fig. 213.—*a*, *b*, *C. concilians* Jörgensen, 1920. East Tasmania. Fig. 214.—*a*, *b*, *C. gibberum* Gourret, 1883. Trial Bay; *c*, *C. gibberum* forma *subaequale* Jörgensen, 1920. Trial Bay. Fig. 215.—*C. lunula* Schimper, 1900. *a*, East Australia; *b*, Western Australia. Fig. 216.—*C. schmidtii* Jörgensen, 1911. *a*, New Guinea; *b*, Trial Bay. Fig. 217.—*C. symmetricum* Pavillard, 1905. *a*, *b*, Trial Bay; *c*, west of Bass Strait. Fig. 218.—*a*, *C. declinatum* Karsten forma *normale* Jörgensen, 1920. Jibbon Cape; *b*, *C. declinatum* forma *brachiatum* Jörgensen, 1920. Jibbon Cape; *c*, *C. declinatum* forma *debile* Jörgensen, 1920. Jibbon Cape. Fig. 219.—*C. axiale* Kofoid, 1907. Jibbon Cape. Fig. 220.—*a*, *b*, *C. euarcuatum* Jörgensen, 1920. Trial Bay.

CERATIUM SYMMETRICUM Pavillard

Fig. 217*a-c*

Ceratium symmetricum Pavillard, 1905.
C. coarctatum Pavillard, 1905.
C. gracile (Gourret) Jörgensen, 1911, including var. *coarctatum* forma *orthoceras* and var. *symmetricum;* Forti, 1922; Böhm, 1931.
C. tripos var. *gracile* Gourret, 1883 non Pouchet, 1883.
nec. *C. tripos* var. *macroceros* forma *gracile* Jörgensen, 1899.
C. tripos var. *gracile* Schröder, 1900 partim.

Medium rather robust form, body much longer than broad, rather flattened; left side strongly convex, rather steep towards apical horn, right side slightly convex. Apical horn a little bent or straight, strong, usually rather long. Base strongly convex, continuous with the evenly curved antapicals. Length, inclination, and curvature of antapicals variable.

According to Steemann Nielsen (1934), *C. gracile* and *C. coarctatum* belong to 1 very variable species. Schiller (1937) agreed and refused to accept Jörgensen's (1911, 1920) differentiation.

Distribution.—Tropical form. Atlantic; south of Africa to 30°N.; Mediterranean; Indian Ocean, 38°S. to Cape Guardafui; Bengal and Sumatra; Pacific, Japan ? South equatorial current, Solomon Is., North I. of New Zealand, east Australia south of 30°S. In this investigation it is recorded from Eden, N.S.W., to Fraser I., Queensland; common in Port Hacking region; Lord Howe I.; Tasman Sea; south coast of New Britain; west of Fremantle, and south coast from Cape Leeuwin to Kangaroo I., S.A., and south of Port Fairy, Vic., where, with *Ornithocercus quadratus*, it indicates the presence of west wind drift.

CERATIUM DECLINATUM Karsten

Fig. 218*a-c*

Ceratium declinatum Karsten, 1907.

C. tripos var. *gracile* B. Schröder, 1900 partim; non Gourret, 1883; nec Pouchet, 1883; nec Jörgensen, 1899; nec Ostenfeld & Schmidt, 1901.

C. tripos gracile Entz, 1902 partim.

C. tripos Pavillard, 1905.

C. gracile Pavillard, 1905.

C. tripos heterocamptum Karsten, 1907 ? partim.

A small delicate species. Body flattened, longer than broad. All 3 horns lying approximately in the body plane. Apical horn usually straight, not quite at right angles to the girdle. Hypotheca somewhat shorter than epitheca, with convex base continuous with the left antapical, while the junction of the right is clearly marked. Left antapical rather short but strong, longer or shorter than body, right longer but more slender than left, bent at base, often bent outwards at tip, but in young forms short, slender, and clearly bent towards apical horn. Girdle poorly developed on the right side.

Distribution.—Warm-water species. Atlantic, from south of Africa to 32°N. Mediterranean, Indian Ocean, Zanzibar, and Arabian Sea, Sunda I., 36-38°S. Pacific, south equatorial current, Solomon Is., and south-east Australia, mainly below 30°S. (Steemann Nielsen 1934). The author has found this species between Trial Bay and Port Hacking, N.S.W.

CERATIUM AXIALE Kofoid

Fig. 219

Ceratium axiale Kofoid, 1907.

Medium-sized species of the Tripos section, with apical horn bent to right, narrowly rounded shoulders and antapicals flexed close to body and distally subparallel to apical. Mid body rotund, base somewhat asymmetrical, convex, right antapical horn nearer body than left, and bends outward distally, longer than left antapical.

Distribution.—A very rare warm-water form. According to Jörgensen (1911) occurs in Atlantic (28°S.); Pacific, 1°N. to 16°S. (Kofoid); Indian Ocean, 4°S. and 25°S. Also recorded from Atlantic by Peters (1932) and from Pacific by Steemann Nielsen (1934), from Solomon Is., south equatorial current, and east Australia and current below lat. 30°S. The author has found it only between Eden and Point Danger, N.S.W., on the east coast, and at 1 station in the Southern Ocean west of King I. (west wind drift).

CERATIUM EUARCUATUM Jörgensen

Fig. 220*a*, *b*

Ceratium euarcuatum Jörgensen, 1920.
C. arcuatum (Gourret) Pavillard, Jörgensen, 1911.
C. tripos var. *arcuatum* Gourret, 1883.
C. tripos var. *gracile* B. Schröder, 1901 partim.
C. arcuatum Pavillard, 1905.
non *C. arcuatum* Cleve, 1900; nec Ostenfeld & Schmidt, 1901; nec Karsten, 1906, 1907; nec Vanhöffen, 1897; nec Jörgensen, 1899; nec Böhm, 1931.

Body flattened, much longer than broad. Base regularly curved, continuous with antapicals. Right antapical small and regularly curved, directed forward from base, longer than or as long as left, often converging at the point towards the thin, almost straight apical horn. Left antapical regularly curved, directed forward from base, converging slightly towards apical or parallel to it. Girdle slightly developed on right, often undiscernible in young forms. Very delicate.

Distribution.—Oceanic, warm-water species. Atlantic, 26°S. to 37°N., Mediterranean, Indian Ocean, 25°S. to Ceylon and Sumatra. Pacific, south equatorial and east Australian current, Solomon Is., east Australia (Steemann Nielsen 1934), not in truly neritic stations. Rare on east Australian coast from Low I. to Port Hacking, N.S.W., in this investigation.

CERATIUM ARIETINUM Cleve

Fig. 221*a*

Ceratium arietinum Cleve, 1900.
C. heterocamptum Ostenfeld & Schmidt, 1901.
non *C. heterocamptum* Paulsen, 1908 = *C. bucephalum* Cleve.
nec *C. bucephalum* var. *heterocamptum* Jörgensen, 1899, 1905.
vix *C. tripos* var. *arcuatum* forma *heterocampta* Jörgensen, 1899.

Medium-sized species, resembling *C. bucephalum.* Apical horn somewhat bent to left at base, then straight, but often bent again slightly left. Left antapical horn evenly curved, usually more or less converging, rarely parallel. Right very strong and evenly curving right to the point, sometimes twisted. Right antapical like left, without further bending.

CERATIUM ARIETINUM forma REGULARE Jörgensen
Fig. 221*a*

Ceratium arietinum forma *regulare* Jörgensen, 1920.

Found in Australasian waters on south-east coast only.

CERATIUM ARIETINUM forma DETORTUM (Stüwe) Jörgensen
Fig. 221*b*, *c*

Ceratium arietinum forma *detortum* (Stüwe) Jörgensen, 1920.

Apical horn strong, bent near tip. Right antapical bent differently from left. Australia, east coast.

CERATIUM ARIETINUM forma GRACILENTUM Jörgensen
Fig. 221*d*

Ceratium arietinum forma *gracilentum* Jörgensen, 1920.

More slender. Like the above form, apical horn only bent at base. Australia, east coast.

CERATIUM ARIETINUM forma VALENS Jörgensen
Fig. 221*e*

Ceratium arietinum forma *valens* Jörgensen, 1911.

Very robust form. Right antapical as for forma *detortum*.

Distribution.—Warm-water species. Atlantic 43°S. to 37°N. Rare in Indian Ocean, 38°S. to 2°S.; Arabian and Red Seas. Pacific, Japan. Recorded by Steemann Nielsen (1934) only from the south equatorial current and east Australian current below 30°S.; Graham and Bronikowsky (1944) found it common in warm water in the Atlantic and Pacific Oceans. Found by the author from Maria I., Tas., to Cape Byron, N.S.W.; and Cape Inscription on west coast of Australia; rare.

CERATIUM AZORICUM Cleve
Fig. 222*a*, *b*

Ceratium azoricum Cleve, 1900.

Small species. Body flat, but curved laterally. Mid body large, epitheca rounded, about equal to hypotheca. Apical horn robust, wide at base, tapering, often winged. Hypotheca deep, base strongly convex or humped, antapicals wide at base, narrowing rapidly to tips, thick-walled on convex side, continuous with base of hypotheca, both directed forwards, slightly diverging to converging. All horns short.

Distribution.—Warm-water species. Atlantic, 31°S. to North Atlantic; Mediterranean. Indian Ocean, rare (8°N.); Pacific Ocean, equatorial current, Solomon Is., New Zealand (North I.), east Australia below 30°S. (Steemann Nielsen 1934). In this investigation on east coast of Australia, Eden, N.S.W., to Moreton Bay, Queensland; on south coast off Albany, W.A., and on west coast (1 station).

CERATIUM LIMULUS Gourret

Fig. 223*a*, *b*

Ceratium limulus Gourret, 1883.
C. tripos var. *limulus* Pouchet, 1883.

Rather small, short-horned, and flattened species. Somewhat resembling *C. azoricum,* but with characteristic humps or bosses on epitheca on each side of usually winged apical horn. Apical horn short, thick, tapering. Hypotheca deep, base rounded, continuous with forwardly directed antapicals. These are wide at base, short, close to body, left may curve over epitheca and turn parallel with apical horn. Body usually strongly sculptured.

Distribution.—Widely distributed in warm Atlantic, 38°S. to 36°N.; Mediterranean; Indian Ocean, 28°S. to Red Sea and Sumatra; Pacific, Japan, Solomon Is. South-east Australia below 30°S. Rare on east Australian coast in this investigation from lat. 34° to 27°S., and in Southern Ocean south of Port Fairy, Vic. Graham and Bronikowsky (1944) considered this a truly oceanic form and its occurrence in onshore waters indicative of the oceanic nature of the water which frequently reaches the coast of east Australia.

CERATIUM PARADOXIDES Cleve

Ceratium paradoxides Cleve, 1900.

Very like *C. limulus,* but without the bosses on each side of the apical horn, but with decided humps. Characterized by irregular or regular-sized polygons as theca markings.

Distribution.—Rare warm-water species. Atlantic to 40°N. and 30½°S., Indian Ocean, Arabian Sea, and to 25°S. off Africa. Pacific, south equatorial stream, rare in south-east Australia from Sydney to Moreton Bay, Queensland (Steemann Nielsen 1934). Not recorded in this investigation.

CERATIUM PETERSII Steemann Nielsen

Fig. 224*a*, *b*

Ceratium petersii Steemann Nielsen, 1934.
C. bucephalum Cleve, Peters, 1932.

This species resembles *C. azoricum,* differing from it in the more widely spread antapicals and the narrower, slightly curved apical horn. In both species the apical horn is usually winged and the girdle poorly defined. It may well be a form of *C. azoricum,* but if so is confined to colder water, in which *C. azoricum* can also occur.

Distribution.—Pacific Ocean, Australia: south-east Tasmania; south-east of New Zealand (Steemann Nielsen). Indicative of sub-Antarctic flora.

CERATIUM LONGINUM Karsten

Fig. 225

Ceratium longinum Karsten, 1906.
C. arcuatum forma *caudata* Karsten, 1906 partim.

Very similar to *C. karstenii* and *C. contortum* forma *subcontortum.* Graham and Bronikowsky (1944) considered *C. longinum* a form of *C. contortum.* Base contour straight or slightly convex, antapical almost or quite continuous with base. Apical strongly displaced at the left, clearly bent to left at base, very long, usually about S-shaped. Frequently with circular lists. Antapicals strongly deflected ventrally, directed obliquely towards the apical horn, often parallel to it; the right usually quite straight and only curved below, the left is evenly bent and diverges again from the apical horn or is bent towards it. The body plane diverges greatly from that of the antapical so that in ventral view the one horn seems much nearer the apical horn than the other. The right antapical arises immediately behind the girdle, more or less distant than in *C. karstenii.*

Distribution.—A rare warm-water form from the Atlantic and Indian Oceans. One example was found in a catch off Trial Bay, N.S.W., with a number of tropical forms, including *Histioneis, Parahistioneis,* and *Heterodinium.*

Section *Platycornia* Jörgensen, 1911

CERATIUM PLATYCORNE von Daday

Fig. 226

Ceratium platycorne von Daday, 1888.
C. tripos var. *aurita* Cleve, 1897.
C. lamellicorne Kofoid, 1908.
C. tripos forma *dilatata,* 1905.
C. dilatatum Kofoid, 1907; non Gourret, 1883.
C. tripos platycorne Karsten, 1907 partim.
C. compressum Gran, 1911.

Rather small, flattened form, characterized by the antapicals, which are more or less flattened in the body plane. Epitheca long, tapering into apical horn, spines may be present on epitheca and horn. Hypotheca rather low, convex. Antapicals parallel with girdle or directed forward curving sharply towards apical, converging, flat. Ends usually blunt, irregular, margin and base thickened and often ridged and toothed. Ridges on antapicals and body. Body punctate.

Distribution.—Tropical, rare, Atlantic 10°N. to 57°N., with Gulf Stream and 48°N. with Florida Stream; Mediterranean; Indian Ocean, 34°N. to Cape Guardafui and Sunda I.; Pacific, Japan, California, south equatorial current, New Zealand (North I.), south-east Australia below 30°S. The author has found examples between Port Hacking, N.S.W. (34°S.) and Point Danger, 1 in the B.A.N.Z.A.R.E. plankton off east Tasmania, and 1 with rather narrow, uniform antapicals in Bass Strait; it is common in the west wind drift south of Port Fairy, Vic.

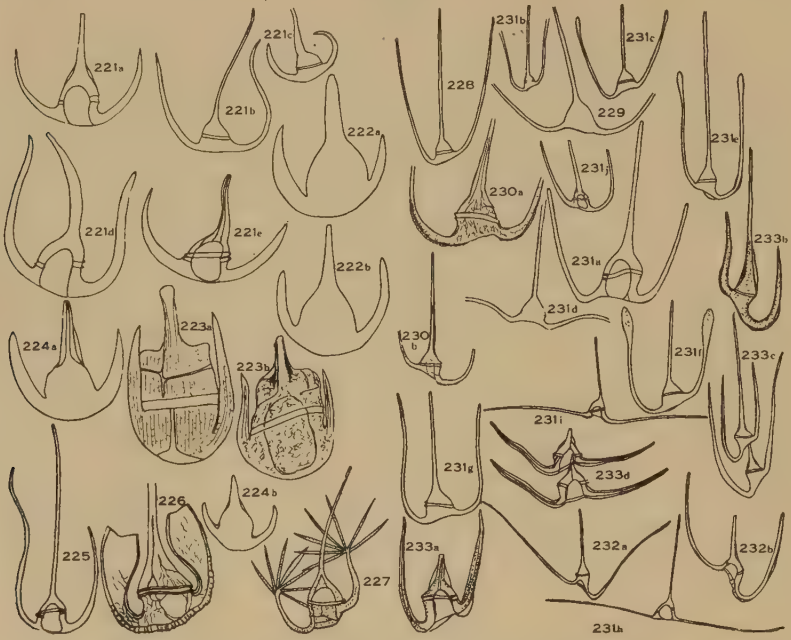


Fig. 221.—*a*, *Ceratium arietinum* forma *regulare* Jörgensen, 1920. Trial Bay; *b*, *c*, *C. arietinum* forma *detortum* (Stüwe) Jörgensen, 1920. Jibbon Cape; *d*, *C. arietinum* forma *gracilentum* Jörgensen, 1920. Jibbon Cape; *e*, *C. arietinum* forma *valens* Jörgensen, 1911. Port Stephens. Fig. 222.—*C. azoricum* Cleve, 1900. *a*, Trial Bay; *b*, south-east of Tasmania (B.A.N.Z.A.R.E.) near convergence. Fig. 223.—*a*, *b*, *C. limulus* Gourret, 1883. Trial Bay. Fig. 224.—*C. petersii* Steemann Nielsen, 1934. *a*, Crescent Head, N.S.W.; *b*, east of Tasmania (B.A.N.Z.A.R.E.). Fig. 225.—*C. longinum* Karsten, 1906 Trial Bay. Fig. 226.—*C. platycorne* von Daday, 1888. East of Tasmania (B.A.N.Z.A.R.E.). Fig. 227.—*C. ranipes* Cleve, 1900. South of Albany, W.A. Fig. 228.—*C. longissimum* (Schröder) Kofoid, 1907. Fig. 229.—*C. longipes* forma *balticum* Ostenfeld, 1903. South-east Tasmania (B.A.N.Z.A.R.E.). Fig. 230.—*C. horridum* Gran, 1902. *a*, Bass Strait-Tasmania form; *b*, Port Hacking form. Fig. 231.—*a*, *C. buceros* forma *tenue* (Ostenfeld & Schmidt) Schiller, 1937. Port Hacking; *b*, *c*, *C. buceros* forma *inclinatum* (Kofoid) Schiller 1937. Port Stephens; *d*, *C. buceros* forma *leptosomum* (Jörgensen) Schiller, 1937. East Tasmania; *e*, *f*, *C. buceros* forma *claviger* (Kofoid) Schiller, 1937. *e*, East of Tasmania (B.A.N.Z.A.R.E.); *f*, Jibbon Cape; *g*, *C. buceros* forma *molle* (Kofoid) Schiller, 1937. Port Hacking; *h*, *C. buceros* forma *tenuissimum* (Kofoid) Schiller, 1937. New Guinea; *i*, *C. buceros* forma *denticulatum* (Jörgensen) Schiller, 1937. Port Hacking. Fig. 232.—*a*, *b*, *C. pavillardii* Jörgensen, 1911. Fig. 233.—*a*, *C. vultur* Cleve, 1900. New Guinea; *b*, *C. vultur* forma *japonicum* (B. Schröder). New Guinea; *c*, off Cape Moreton; *d*, *C. vultur* forma *sumatranum* (Karsten) Steemann Nielsen, 1934. Trial Bay.

Ostenfeld (1931) considered *C. platycorne* a tropical form which becomes *C. compressum* in unfavourable (cool) water, in which case *C. compressum* should be transferred from Section Tripos to Section Platycornia.

Section *Palmata* (Pavillard) Jörgensen, 1911

CERATIUM RANIPES Cleve

Fig. 227

Ceratium ranipes Cleve, 1900.
Ceratium palmatum var. *ranipes* Cleve, Jörgensen, 1911; Forti, 1922.
C. tripos var. *digitatum* Lemmermann, 1900 = Schütt, 1892.
C. tripos var. *macroceras* forma *palmata* Schröder, 1900.
C. tripos var. *furcellata* Lemmermann, 1900.

Rather small species. Epitheca with convex sides. Girdle not perpendicular to apical horn. Apical horn bent at base, slightly curved to straight, usually toothed. Hypotheca about equal to epitheca, base making an acute angle with girdle, usually strongly toothed, convex. Antapicals beginning parallel with base, curving towards apical horn, toothed, left diverging or parallel, right converging, frequently crossing apical horn and at times ending parallel with it, both antapicals terminating in 5-7 fingers. Theca with spinelets and ridges; plates obvious, raised at junctions.

Distribution.—Widely distributed warm-water species. Atlantic, southern tip of Africa, 38°S. to 49°N., Mediterranean, Indian Ocean, 12°S. to Ceylon, Gulf of Aden to 25°S. Pacific, Japan, south equatorial current, New Zealand (North I.), south-east Australia. The author has found this species on the east coast from Moreton Bay, Queensland, to Port Hacking, N.S.W., and in the south-west of Western Australia, where it was numerous in a few hauls. This suggests a tropical tongue reaching south-west Australia, but not impinging on the Western Australian coast north of Cape Naturaliste.

CERATIUM LONGISSIMUM (Schröder) Kofoid

Fig. 228

Ceratium longissimum (Schröder) Kofoid, 1907.
C. tripos var. *macroceros* forma *longissima* Schröder, 1900.
?*C. flagelliferum* var. *angusta* Zacharias, 1906.

Medium-sized species with unusually long, slender, often parallel horns. Apical horn slightly bent at base, then straight. Body small.

Epitheca oblique, rather high (long) with strongly convex left and slightly convex right contour. Base rather longer than almost straight but very oblique side contour. Base contour not depressed, slightly convex, almost continuous with left antapical. Antapical sharply bent forward, more or less parallel with apical, but a little undulating and somewhat diverging at apex. Left antapical diverted obliquely backwards, but very sharply bent forward, evenly curved at base. Right antapical transverse, bent at emergence, somewhat longer than the left. Theca with small but strong ridges and low encircling wings at the proximal part of the horns visible on the base.

Distribution.—Rare tropical form. Atlantic, equator, Mediterranean, Pacific, equatorial current, and east Australian current. One specimen found off Point Danger, south Queensland, 5.i.1941.

CERATIUM LONGIPES (Bailey) Gran

Ceratium longipes (Bailey) Gran, 1902.
Peridinium tripos Ehrenberg, 1934 partim.
P. longipes Bailey, 1855.
C. tripos var. *tergestina* Hensen, 1887; Schütt, 1892.
C. tripos var. *longipes* Cleve, 1897.
C. longipes Gran, 1902.
C. longipes forma *oceanica* Ostenfeld, 1903.
C. horridum Gran, Wailes, 1928.

Very like many forms of *C. horridum* Gran, from which it differs in its more strongly bent apical horn. The almost similar *C. arcticum* has strongly spreading horns, and is considered identical by Graham and Bronikowsky (1944). There is little difference in the base contour, in which the left is normally more clearly oblique than the right (the opposite is the case with *C. horridum*).

CERATIUM LONGIPES forma BALTICUM Ostenfeld

Fig. 229

Ceratium longipes forma *balticum* Ostenfeld, 1903.

Slender, long, thin-horned, and smooth.

The form shown is ascribed to *C. longipes*, but could almost as easily have been ascribed to *C. arcticum.*

Distribution.—In North Sea and Baltic early in the year. Australia: south-east of Tasmania only.

CERATIUM HORRIDUM Gran

Fig. 230*a*, *b*

Ceratium horridum Gran, 1902.
C. intermedium (Jörgensen) Jörgensen, 1905, 1911; Paulsen, 1908.
C. tripos var. *macroceras* forma *intermedia* Jörgensen, 1899.
C. tripos var. *scotia* forma *horrida* Ostenfeld, 1900.
C. tripos Reedecke, 1902.
C. batavum Paulsen, 1908.
vix. *C. tripos* var. *horrida* Cleve, 1896.

Rather small, short-horned, robust, very variable species. Differs from *C. longipes* in the straight apical horn, and the obvious angle that the curved right antapical makes with the base contour. Direction and curvature of antapicals very variable. Apical horn may be winged and toothed, teeth on antapicals may be present; body usually sculptured.

C. longipes, C. horridum, and *C. buceros* are not easily distinguished, and there has been considerable confusion in the literature; Jörgensen (1905, 1911) separated *C. intermedium* from *C. horridum,* but in 1920 reunited *C. intermedium, C. tenue,* and *C. molle* into *C. horridum* Gran. As Gran's form is a North Atlantic one, he separated 2 subspecies, *horridum* Gran and *buceros* Zacharias, the latter containing 2 varieties, var. *molle* (Kofoid) and var. *tenue* (Ostf. & Schmidt). Schiller (1937) quoted Böhm (in lit.) as suggesting the separation of the 2 subspecies with the forms *molle, tenue, leptosomum,* and *tenuissimum.* Schiller adopted this suggestion. *C. horridum* is then confined to the cold-water form of the North Atlantic, while the tropical forms become *C. buceros.* Graham and Bronikowsky (1944) united *C. molle* and *C. claviger* with *C. horridum* and separated *C. tenue, C. tenuissimum,* and *C. inclinatum* as *C. tenue.* Both morphology and distribution indicate that Schiller's divisions are preferable.

Distribution.—North Atlantic. The author has found *C. horridum* in Tasmanian waters, in Bass Strait, and at times as far north as Sydney. It appears to be a cold and cool-temperate form and to indicate the presence of a water mass derived from the south, and probably there is a closed biological area in the Tasmanian-Bass Strait region.

The author inclines to the present view as this species is not listed from the sub-Antarctic in "Discovery" reports and was not seen in some Heard I. plankton shown to the author by Mr. Ealey, or in the B.A.N.Z.A.R.E. material.

CERATIUM BUCEROS (Zacharias) Schiller

Ceratium buceros (Zacharias) Schiller, 1937.
C. horridum Gran. Jörgensen, 1920 partim.
C. tenue (Ostenfeld & Schmidt) Jörgensen, 1911, 1901.
C. patentissimum Karsten, 1906.
non *C. patentissimum* Ostenfeld & Schmidt, 1901.
C. tripos inversum Karsten, 1907.
C. tripos inclinatum var. *minor* Karsten, 1907.
C. inclinatum Kofoid, 1907.
C. buceros Zacharias, 1906.
C. tripos volans forma *recurvata* Karsten, 1906.
C. tripos buceros Karsten, 1907 partim.
C. leptosomum Jörgensen, 1911.
C. claviger Kofoid, 1907, Jörgensen, 1911.
C. mollis Kofoid, 1907, Jörgensen, 1911.
C. tripos flagelliferum var. *angusta* Karsten, 1906 partim.
C. undulatum Schröder, 1906 partim.

A variable but long-horned warm-water species with a small body. Body longer than broad, base markedly convex, sometimes rather sunken. All horns very thin, distally truncate, often widened, club-shaped.

CERATIUM BUCEROS forma TENUE (Ostenfeld & Schmidt) Schiller

Fig. 231*a*

Ceratium buceros forma *tenue* (Ostenfeld & Schmidt) Schiller, 1937.
C. tenue (Ostenfeld & Schmidt) Jörgensen, 1911.

Epitheca strongly convex opposite girdle. Hypotheca slightly longer, left side concave, oblique. Base convex, reentrant to right near girdle. All horns thin, often wider at ends, truncate or clavate, antapicals diverging.

Distribution.—Tropical Atlantic, 29°S. to North Atlantic; Mediterranean; Indian Ocean, Red Sea to Zanzibar, Sumatra, Gulf of Siam, 38°S., Pacific, California, Japan, equatorial current and south to 37°S., but not inside Great Barrier Reef. East coast of Australia from Maria I., Tas., to Sandy Cape, Queensland; common estuarine form in Port Hacking, N.S.W., Western and South Australia north-west at least to Cape Inscription; also in Bass Strait and Storm Bay, Tas.

CERATIUM BUCEROS forma INCLINATUM (Kofoid) Schiller

Fig. 231*b*, *c*

Ceratium buceros forma *inclinatum* (Kofoid) Schiller, 1937.
C. inclinatum Kofoid, 1907.

Post indentation slight, antapicals diverging at an acute angle, incurved distally with contracted but still open tips which may be slightly clavate. Intergrades with forma *molle* and forma *claviger*.

Distribution.—Warm-water form. Atlantic (de Sousa e Silva 1949). East coast of Australia from Maria I. to Moreton Bay, Queensland, New Guinea, New Britain, Solomon Is., Lord Howe I., and Tasman Sea. West coast, Cape Inscription, and north-west coast. South coast, Albany to Israelite Bay, W.A.

CERATIUM BUCEROS forma LEPTOSOMUM (Jörgensen) Schiller

Fig. 231*d*

Ceratium buceros forma *leptosomum* (Jörgensen) Schiller, 1937.
C. leptosomum Jörgensen, 1911.

Markedly resembling *C. carriense*. Epitheca rather oblique, apical horn medium, contour convex, left side of hypotheca straight or slightly convex (as *C. carriense*). Hypotheca indented basally, almost continuous with the oblique rearward-pointing junctions of antapicals. All horns rather thick in the proximal part, then very thin and widened at ends, truncate apical curved at base, left antapical with a relatively long basal piece directed obliquely left and to the rear, then evenly curved, then in the outer $\frac{2}{3}$ almost linear, slightly incurved at the end. Right antapical with a similar but shorter basal piece, directed to the right and backwards, then sharply bent and straight pointing to the right and forward, base of antapicals and base finely toothed and winged.

Distribution.—A few forms recorded from the Atlantic between the Azores and West Indies. Rare on east coast of Australia, found off Point Danger, N.S.W.

CERATIUM BUCEROS forma CLAVIGER (Kofoid) Schiller

Fig. 231*e*, *f*

Ceratium buceros forma *claviger* (Kofoid) Schiller, 1937.

Apical horn straight, body small, base slightly or not indented. Antapicals parallel or slightly diverging, ends swollen, clavate, may be bifurcate.

Distribution.—Rare, warm-water form. Recorded by de Sousa e Silva from Portugal, by Kofoid from California, Steemann Nielsen from south equatorial current, New Zealand (North I.), and east Australia below 30°S. Found in this investigation between Port Hacking and Port Stephens, N.S.W.

CERATIUM BUCEROS forma MOLLE (Kofoid) Schiller

Fig. 231*g*

Ceratium buceros forma *molle* (Kofoid) Schiller, 1937.

All 3 horns parallel, base slightly indented, antapicals delicate and somewhat flexible, may be undulate.

Distribution.—Rare in Atlantic, Danish West Indies, Mediterranean, Indian Ocean, Red Sea, Pacific, San Diego. Equatorial current, New Zealand (North I.), east Australia below 30°S. The author has found this form rarely on the east coast of Australia from Maria I., Tas., to Moreton Bay, Queensland; New Guinea; south coast of Western Australia, and west coast from Cape Leeuwin to Cape Inscription, and once from Storm Bay, Tas.

CERATIUM BUCEROS forma TENUISSIMUM (Kofoid) Schiller

Fig. 231*h*

Ceratium buceros forma *tenuissimum* (Kofoid) Schiller, 1937.

Base little indented, antapicals spread laterally with slight major flexures (right 50-80° and left about 90° with apical), straight or slightly reflexed posteriorly. Karsten's form *C. tr. volans* forma *recurvatum* was assigned by Kofoid to this species.

CERATIUM BUCEROS forma DENTICULATUM (Jörgensen) Schiller

Fig. 231*i*

Ceratium buceros forma *denticulatum* (Jörgensen) Schiller, 1937.

Distribution.—Eastern Bass Strait to Sandy Cape, Tasman Sea, New Guinea, New Britain, and Solomon Is. Not recorded from South Australian waters nor from Western Australia south of Cape Inscription.

CERATIUM PAVILLARDII Jörgensen

Fig. 232*a*, *b*

Ceratium pavillardii Jörgensen, 1911.
C. vultur Pavillard, 1905 non Cleve.

Rather large form related to *C. vultur*. Epitheca almost triangular with convex left and almost straight, very oblique left side. Hypotheca longer than epitheca with straight, very oblique left side. Base steep, slightly indentate, oblique with girdle. All horns in proximal portion robust, thin at tips. Apical rather long, left antapical directed obliquely backwards and to the left, then near its attachment bent at right angles and directed obliquely forward and to the left. Right antapical transverse at base, then evenly bent forward, almost straight distally and both horns diverging somewhat distally. Theca structure very robust, with numerous large or small irregularly curved lines and along the horns, long and narrow, not clearly toothed wings. Narrow lists on antapicals with a spine-like list evident at the bend of the left antapical.

Distribution.—Rare warm-water form. Atlantic, 20°S. to 33°N.; Mediterranean; Indian Ocean, 26°30′S.; Pacific, Japan. Not recorded by Steemann Nielsen. A form which the author ascribes to *C. pavillardii* forma *delicatula* forma nov., is moderately common in a few samples from Eden to Moreton Bay, common at times in Port Hacking, N.S.W., and rare in Storm Bay, Tas., in New Guinea and Solomon Is., on the south coast from Albany, W.A., to Kangaroo I., S.A., but is rare on the southwest coast of Western Australia. In this form, which is rather delicate, the right antapical begins opposite the apical horn and continues for a shorter or longer distance before curving rapidly forward, parallel or diverging from the apical horn, the curvature being usually more gradual than in *C. pavillardii* as described by Jörgensen. The left antapical is typical of *C. pavillardii*.

CERATIUM VULTUR Cleve

Fig. 233*a*

Ceratium vultur Cleve, 1900.
C. robustum Ostenfeld & Schmidt, 1901.
C. tripos forma *neglecta* Karsten, 1905 partim.
non *C. neglectum* Ostenfeld, 1906.
C. robustum Schröder, 1906.
C. tripos robustum Karsten, 1907.

Robust form with strongly developed wings on apical horn, often on epitheca, base, and antapicals. Base straight or slightly concave, making a steep angle, sometimes almost at right angles with girdle. Apical horn short or long and curved, at times almost sigmoid. Left antapical starts at right angles to apical horn, then turns very sharply forward, may be parallel to or diverge somewhat from apical. Right antapical pointing more or less backwards at base, then turning sharply and running more or less parallel to apical horn. Sculpture strong on body and horns.

Distribution.—Rather rare warm-water form. Atlantic, 28°S. to 20°N. Indian Ocean, 27°S. to Aden and Sumatra. Celebes, Pacific, East China Sea, and Sea of Japan, equatorial current, 3 stations (Steemann Nielsen 1934), northern Queensland. Rare on east Australian coast and in New Guinea.

CERATIUM VULTUR forma JAPONICUM (B. Schröder)

Fig. 233*b*, *c*

Ceratium vultur forma *japonicum* (B. Schröder).
C. japonicum Schröder, 1906.
C. vultur var. *japonicum* (Schröder) Jörgensen, 1911.

Differs from type in its long horns. Antapicals sharply bent, then parallel to apical. Australia: rare on east coast from Port Hacking, N.S.W., to New Guinea.

CERATIUM VULTUR var. SUMATRANUM (Karsten) Steemann Nielsen

Fig. 233*d*

Ceratium vultur var. *sumatranum* (Karsten) Steemann Nielsen, 1934.
C. vultur Ostenfeld & Schmidt, 1901, non Cleve.
C. tripos var. *neglecta* Karsten, 1905 partim.
C. tripos vultur Karsten, 1907.
C. tripos vultur var. *sumatranum* Karsten, 1907.
C. sumatranum (Karsten) Jörgensen, 1911; Böhm, 1931.

Body form and apical horn identical with type, antapicals arising as in type, but more spreading, often undulate, very robust, may be toothed. Body and horns sculptured. Chain-forming.

Distribution.—Tropical form. Atlantic, 28°S. to 20°N.; Indian Ocean, 25°S. to Aden, Sumatra, Celebes; Pacific, East China Sea and Sea of Japan (Jörgensen 1911), equatorial current, but not south of it (Steemann Nielsen 1934). In this investigation it was found quite commonly at times, east coast, Eden, N.S.W., to Moreton Bay, Queensland. Solomon Is.; west coast, Fremantle, W.A., to north-west coast of Australia. South coast, eastern part of Great Australian Bight, not found in western portion of Bight.

CERATIUM REFLEXUM Cleve

Ceratium reflexum Cleve, 1900.

Medium form with unusual habit. Body like *C. vultur*, rather flattened. Epitheca broad and low. Hypotheca almost twice as long as epitheca. All 3 horns, especially the apical, widened and thick-walled at base, thin-walled, narrow at apex with more or less evident somewhat toothed lists. Girdle lists very strongly developed. Left antapical directed obliquely backwards, then sharply backwards and somewhat twisted.

Right antapicals as long or longer, transverse at base, then sharply bent forward, diverging at 20-15° from apical. Theca structure usually obvious with small but robust twisted ribs and small, conspicuous pores.

Distribution.—Rare, tropical form. Atlantic, rare 38°N. to 19°S. Indian Ocean, Red Sea, and along equator to Sumatra, south to 25°S., 50°E. South equatorial stream, Pacific, in 1 sample from east Australian coast by Steemann Nielsen (1934). Not found in present investigations.

CERATIUM HEXACANTHUM Gourret

Fig. 234*a, b*

Ceratium hexacanthum Gourret, 1883.
C. reticulatum (Pouchet) Cleve, 1903; Paulsen, 1908; Jörgensen, 1911; Pavillard, 1916; Forti, 1922.
C. tripos var. *reticulata* Pouchet, 1883.
C. tripos var. *inaequale* Gourret, 1883.
non *C. reticulatum* Imhof, 1883.

Large and very long-horned form with concave body. Apical horn twisted or rather sharply bent. Left antapical rather small at base, bent rearwards and strongly ventrally, then very straight and converging towards apical or hair-like and narrowly curved. Right antapical at first at right angles to apical, then bent and twisted, very often whip-like, long, and may be spirally curved. Body regularly reticulate with large pattern, which is characteristic.

Distribution.—Warm-water form. Atlantic, numerous from 28°S. to 58°N., Indian Ocean, 26°S. to Red Sea and Sumatra. Pacific, Japan, equatorial current. Steemann Nielsen recorded the species from 2 stations off New South Wales. The author has found it on the east coast of Australia from Maria I., Tas. (August) to Sandy Cape, Queensland, Tasman Sea, Lord Howe I., Solomon Is., south coast from west of King I., from Victor Harbour, S.A., to Israelite Bay and off Rottnest I. in southwest. Forms with whip-like antapicals are common.

CERATIUM MASSILIENSE (Gourret) Jörgensen

Ceratium massiliense (Gourret) Jörgensen, 1911.
C. tripos var. *massiliense* Gourret, 1883.
C. aequatoriale Schröder, 1906.
C. volans Cleve fide Schröder, 1906.
C. undulatum Schröder, 1906.
C. tripos var. *macroceros* forma *undulata* Schröder, 1910.
C. volans Ostenfeld & Schmidt, 1901.
C. tripos macroceroides Karsten, 1906 partim.
non *C. macroceros* (Ehr.) Cleve, 1901; Pavillard, 1907, 1916.
C. ostenfeldii Kofoid, 1907.
C. tripos macroceros var. *crassa* Karsten, 1907.
C. tripos robustum var. Karsten, 1907.

Large, long-horned, very variable form. Epitheca oblique, base contour almost straight or slightly concave. Antapicals arising almost at right angles to each other, than bending sharply through a right angle, becoming straight and more or less diverging or equally curved, wavy with somewhat incurved ends. Left horn with long and often with 2 small fins on base. Jörgensen (1920) gave a large number of forms of which Schiller (1937) accepted 3.

Distribution.—Warm-water form, also in temperate regions, littoral and pelagic. Very widely distributed.

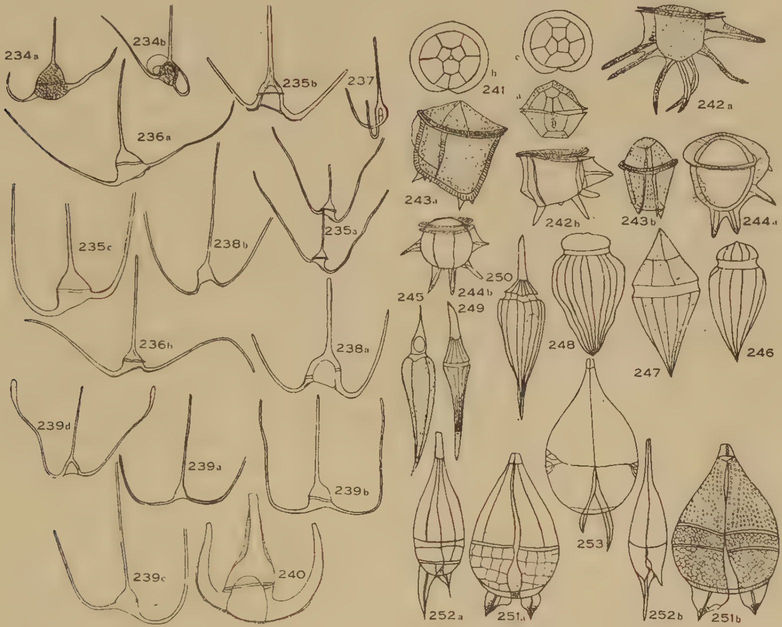


Fig. 234.—*a, b, Ceratium hexacanthum* Gourret, 1883. Jibbon Cape. Fig. 235.—*a, C. massiliense* forma *macroceroides* (Karsten) Jörgensen, 1911. Port Macquarie; *b, C. massiliense* forma *armatum* (Karsten) Jörgensen, 1911. Port Stephens; *c, C. massiliense* forma *protuberans* (Karsten) Jörgensen, 1911. Port Macquarie. Fig. 236.—*a, C. carriense* forma *volans* (Cleve) Jörgensen, 1911. Trial Bay; *b, C. carriense* forma *ceylanicum* (B. Schröder) Jörgensen, 1911. Lord Howe I. Fig. 237.—*C. deflexum* (Kofoid) Jörgensen, 1911. Jibbon Cape. Fig. 238.—*a, C. macroceros* (Ehrenberg) Cleve, 1900. New Guinea; *b, C. macroceros* subsp. *gallicum* (Kofoid) Jörgensen, 1911. Port Hacking. Fig. 239.—*a, C. trichoceros* (Ehrenberg) Kofoid, 1908. Port Hacking; *b, C. trichoceros* var. *contrarium* (Gourret) Schiller, 1937. Port Hacking; *c, C. trichoceros* forma *claviceps* Schröder, 1906. Port Hacking. Fig. 240.—*C. compressum* ? Gran, 1902. Port Hacking. Fig. 241.—*a-c, Goniodoma polyedricum* (Pouchet) Jörgensen, 1899, showing form and plate arrangement. *a*, Ventral view; *b*, epitheca; *c*, hypotheca. Fig. 242.—*a, b, Ceratocorys horrida* Stein, 1883. Port Hacking. Fig. 243.—*a, b, C. armata* (Schütt) Kofoid, 1910. *a*, Side view; *b*, sagittal view. Fig. 244.—*a, b, C. gourreti* Paulsen, 1930. Crowdy Head. Fig. 245.—*Oxytoxum scolopax* Stein, 1883. Fig. 246.—*O. turbo* Kofoid, 1907. Fig. 247.—*O. diploconus* Stein, 1883. Fig. 248.—*O.* sp. Jibbon Cape. Fig. 249.—*O. gigas* Kofoid, 1907. Fig. 250.—*O. subulatum* Kofoid, 1907. Fig. 251.—*a, Podolampas bipes* Stein, 1883. Moreton Bay; *b, P. bipes* forma *reticulata* (Kofoid) Schiller, 1937. Trial Bay. Fig. 252.—*a, b, P. palmipes* Stein, 1883. Fig. 253.—*P.* sp. Jibbon Cape.

CERATIUM MASSILIENSE forma MACROCEROIDES (Karsten) Jörgensen
Fig. 235*a*

Ceratium massiliense forma *macroceroides* (Karsten) Jörgensen, 1911.

Type form.

Distribution.—Steemann Nielsen recorded this form from the warmest part of the south equatorial current (temp. over 26°C). In this investigation forma *macroceroides* occurred from Babel I. (Bass Strait) to Moreton Bay, Queensland, and on the west and south coast, but not in Bass Strait or south Tasmanian waters. A major constituent of the Western Australian plankton and characteristic of it.

CERATIUM MASSILIENSE forma ARMATUM (Karsten) Jörgensen
Fig. 235*b*

Ceratium massiliense forma *armatum* (Karsten) Jörgensen, 1911.
C. massiliense var. *armatum* Jörgensen, 1911.
C. tripos macroceros forma *armata* Karsten, 1905.
C. tripos longipes forma *ventricosa* Karsten, 1906; non Ostenfeld.
C. tripos longipes var. *cristata* Karsten, 1907.

Short-horned and more robust, with toothed wings on apical and epitheca and also on base and hypotheca.

Distribution.—Rare, accompanying forma *protuberans* in temperate waters (Steemann Nielsen 1934). Rather rare on east coast of Australia (New South Wales).

CERATIUM MASSILIENSE forma PROTUBERANS (Karsten) Jörgensen
Fig 235*c*

Ceratium massiliense forma *protuberans* (Karsten) Jörgensen, 1911.
C. tripos protuberans Karsten, 1906.
?*C. tripos tergestinum* Karsten, 1906; non Schütt.
C. tripos longipes Karsten, 1907 partim.
C. tripos flagelliferum var. *crassa* Karsten, 1907.
C. massiliense var. *protuberans* (Karsten) Jörgensen, 1911, 1920; Forti, 1922.
C. protuberans (Karsten) Paulsen, 1930.

Differs from type in the left antapical being less clearly separated from the base, body more rounded; intergrades join in to the type. Recorded by Steemann Nielsen from temperate waters off New Zealand, replacing forma *macroceroides*.

Distribution.—More common on the eastern than the western coast of Australia.

CERATIUM CARRIENSE Gourret

Ceratium carriense Gourret, 1883.
C. tripos var. *massiliense* Gourret, 1883 partim.
C. volans Pavillard, 1905.
C. massiliense Pavillard, 1907.

"This species is so tangled with *C. massiliense* that one can confuse them" (Jörgensen 1911). "It can be differentiated from the robust forms of *C. massiliense* only by the sunken base contour and the angular junction therewith of the left antapical, also by the more curved basal portion of these horns and the wide more spreading right horn, of which the more proximate part makes a large obtuse angle with the adjacent part. In these points, however, both forms are very variable, hence the countless varieties in which the characters of both are mixed (see for example figs. 17, 18 in Böhm, 1931, and our fig. 464*b*). It seems very natural that Gourret described both species as one." Translation of Schiller (1937).

There seems less reason for dividing *C. carriense* from *C. massiliense* than for dividing *C. molle, C. claviger, C. tenue,* and *C. tenuissimum,* which Schiller regarded as 1 species, *C. buceros.* The distribution of the 2 species is similar, and it is probable that they form varieties of a single species. Steemann Nielsen recorded that *C. massiliense* produces forms in neritic situations that closely resemble the type form of *C. carriense.* The separation of 3 forms, *volans, hundhausenii,* and *ceylanicum,* appears valid despite Schiller's argument. Forma *hundhausenii* is commoner than forma *volans* or forma *ceylanicum* in many oceanic hauls east of Australia, but has not been found to the west or south of this country. It is frequently found with forma *volans,* thereby discounting Schiller's theory that the curving is due to the fixative.

CERATIUM CARRIENSE forma VOLANS (Cleve) Jörgensen

Fig. 236*a*

Ceratium carriense forma *volans* (Cleve) Jörgensen, 1911.
C. volans Cleve, 1900; Pavillard, 1931.
C. patentissimum Ostenfeld & Schmidt, 1901; Pavillard, 1907.
C. tripos var. *volans* forma *strictissima* Karsten, 1906; Pavillard, 1916, 1923; Forti, 1922.

A very long-horned form with spreading antapicals.

Distribution.—In Australian waters, east coast, Maria I. to Sandy Cape, New Guinea, Solomon Is. West coast, Rottnest I. to NW. Australia; South Australia, Kangaroo I. region. Not recorded from Great Australian Bight.

CERATIUM CARRIENSE forma CEYLANICUM (B. Schröder) Jörgensen

Fig. 236*b*

Ceratium carriense forma *ceylanicum* (B. Schröder) Jörgensen, 1911.
C. ceylanicum Schröder, 1906; Pavillard, 1931.
C. elegans Schröder, l.c.

Differs from forma *volans* in the ends of both antapicals being bent backwards, often very strongly.

CERATIUM CARRIENSE forma HUNDHAUSENII (Schröder)

Ceratium carriense forma *hundhausenii* (Schröder)
C. hundhausenii Schröder, 1906.

Antapicals very strongly recurved away from apical, forming a semicircle or a circle.

Distribution.—East coast of Australia from Montague I., N.S.W., to Moreton Bay, Queensland. Very common in New Guinea waters, Tasman Sea, and Lord Howe I. Collected from 29 stations in this region, all off shore. Not found in South or Western Australian waters.

C. carriense is recorded from Atlantic, 28°S. to 40°N.; Mediterranean; Indian Ocean from 35°S. to Red Sea and Sumatra; Pacific, Japan, equatorial current, Solomon Is., and east Australia.

CERATIUM DEFLEXUM (Kofoid) Jörgensen

Fig. 237

Ceratium deflexum (Kofoid) Jörgensen, 1911.
C. macroceros deflexum Kofoid, 1907.
C. tripos macroceros Karsten, 1907 partim.
C. californiense Karsten, 1907.
C. recurvatum Schröder, 1906.

Very like *C. macroceros*. Base indentation and body shape similar. Antapicals deflected markedly ventrally, distally straight, 1 or both may be parallel with apical or at right angles thereto.

Distribution.—A rare tropical species not recorded from Atlantic. Indian Ocean, Red Sea to Sumatra, to 25°S., South China Sea, east coast of Malacca, Gulf of Siam, East China Sea, Formosa, Foochow, Boeton Strait; Pacific, Japan, California. According to Steemann Nielsen, occurred in south equatorial stream, east Australian current, and Great Barrier Reef, rare on east coast of Australia, not in Solomons or New Zealand waters. The author records 1 example from Jibbon Cape, N.S.W. (lat. 34°S.) on 27.iii.1943.

CERATIUM MACROCEROS (Ehrenberg) Cleve

Fig. 238*a*

Ceratium macroceros (Ehrenberg) Cleve, 1900.
non Lebour, 1925 = *C. horridum?*
Peridinium macroceros Ehrenberg, 1840.
Ceratium tripos var. *macroceros* Claparède & Lachmann, 1859; Gourret, 1883; Schroder, 1900 (partim); Entz, 1905.
C. tripos var. *scotia* Schütt, 1892 partim.
C. gallicum Kofoid, 1907.
C. californiense Kofoid, 1907.
C. tripos macroceros var. *tenuissima* Karsten, 1907.

Medium-sized, very long-horned species. Base contour almost straight, forming an obtuse angle at each side with antapicals which point rearward, more or less diverging, then sharply curved forward, proximal parts diverging, or parallel to apical horn. Chromatophores numerous.

Distribution.—In temperate waters in all oceans and not completely absent in cold water. Rarer in tropical waters, where it is replaced by *C. gallicum,* according to Jörgensen (1911) and Ostenfeld (1931). It was found widely distributed in Victorian waters and Bass Strait and on the coast of south-east Australia as neritic form, overlapping with subsp. *gallicum* in the Sydney region.

CERATIUM MACROCEROS subsp. GALLICUM (Kofoid) Jörgensen

Fig. 238*b*

Ceratium macroceros subsp. *gallicum* (Kofoid) Jörgensen, 1911.
Ceratium gallicum Kofoid, 1907.
C. californiense Kofoid, 1907; Pavillard, 1931.

A delicate species with deeply indented base, left antapical posterior for some distance before curving forward, both antapicals convex outwardly. Body smaller and more rotund than type, antapicals may be very long.

Distribution.—Abundant warm-water species. Atlantic, South of Africa to north end of Florida stream; Mediterranean; Indian Ocean, 25°S. to Arabian Sea and Sumatra, Boeton Strait; Pacific, Japan, California, general in Pacific. In this investigation this species was found to be general in distribution except in the Victorian-Tasmanian region.

CERATIUM TRICHOCEROS (Ehrenberg) Kofoid

Fig. 239*a*

Ceratium trichoceros (Ehrenberg) Kofoid, 1908.
Peridinium trichoceros Ehrenberg, 1873.
Ceratium flagelliferum Cleve, 1900.
C. tripos flagelliferum Karsten, 1907 partim. forma *crassa* Karsten, 1907.

All 3 horns usually very thin and long, their ends approximately parallel. Antapicals either very thin and long or rather shorter and thicker. Left antapical has normally a very short, more or less evident basal piece from which it is sharply directed back and left and then gently bent forward in a large even bend, the distal end straight or undulate. Right horn like the left but without bend at base.

CERATIUM TRICHOCEROS var. CONTRARIUM (Gourret) Schiller

Fig. 239*b*

Ceratium trichoceros var. *contrarium* (Gourret) Schiller, 1937.
C. contrarium (Gourret) Pavillard, Jörgensen, 1920; Pavillard, 1905, 1931; Böhm, 1931; Peters, 1932; Steemann Nielsen, 1934.
C. inflexum (Gourret) Kofoid, Jörgensen, 1911.
C. tripos var. *inflexum* Gourret, 1883.
C. tripos var. *typicum* Gourret, 1883.
C. tripos var. *gourretii* Lemmermann, 1900.
C. tripos var. *contrarium* Gourret, 1883.
C. flagelliferum Cleve, 1901 partim.

C. flagelliferum var. *filiformis* Okamura & Nishikawa, 1904.

C. tripos var. *macroceros* forma *claviceps* Schröder, 1900. forma *undulata* Schröder, 1900 partim?

C. tripos flagelliferum forma *angusta* Karsten, 1906. var. *undulata* Karsten, 1907.

vix. *C. inflexum* Schröder, 1906.

This variety differs from the type in the similar junctions of both antapicals with the base and absence of the 1st bend in the left horn. It also has a larger body.

CERATIUM TRICHOCEROS forma CLAVICEPS Schröder

Fig. 239*c*

Ceratium trichoceros forma *claviceps* Schröder, 1906.

This form has long, strongly undulate antapicals with club-shaped ends.

Distribution.—Widely distributed warm-water form. Atlantic 28°S. to north end of Florida stream, Mediterranean, Indian Ocean, Red Sea to east of Malacca, Zanzibar, East China Sea, Formosa, Pacific, Japan, equatorial current, Solomon Is., New Zealand (North I.), east Australia. The author has found, as did Steemann Nielsen, that this is the most numerous and most widely distributed form in the South-West Pacific. It is also very numerous in South and West Australian waters, but in the latter is usually greatly outnumbered by *C. massiliense* forma *macroceroides.* In the present investigation from Cape Howe north to New Guinea, Solomon Is., Tasman Sea, Lord Howe I., north Australia, Western and South Australia to Cape Northumberland. Not found in Bass Strait or Tasmanian waters, except for 1 example from the east end of the Ninety Mile Beach, Vic., and 1 from the tropical tongue off Maria I., Tas., in August. One example of forma *claviceps* from eastern Australia near Sydney, 8.i.1941.

CERATIUM COMPRESSUM ? Gran

Fig. 240

Ceratium compressum? Gran, 1902.

A single example of a form (Fig. 240) resembling *Ceratium compressum* Gran, 1902 was found in plankton from Port Hacking collected 9.viii.1943. It differed from the type in having open antapical horns. As it was accompanied by *C. horridum,* which the author regards as an indicator of cool-temperate water, and occurred in the winter months, it may well be a cold-water form of *C. platycorne,* as has been suggested for *C. compressum.* The body form is essentially that of a member of the Tripos section.

Genus GONIODOMA Stein

Goniodoma Stein, 1883.

Cell polygonal or rounded: girdle equatorial, with compressed lists supported by spines: ventral area short and broad, made up of several platelets. Apical pore with apical closing plate; plate formula 3′ or 4′ (?) 7″ 6*g*. 5‴ 3″″. Type species *G. polyedricum* (Pouchet) Jörgensen, 1899.

GONIODOMA POLYEDRICUM (Pouchet) Jörgensen

Fig. 241*a-c*

Goniodoma polyedricum (Pouchet) Jörgensen, 1899.
Peridinium polyedricum Pouchet, 1883.
Goniodoma acuminatum Stein, 1883; Butschli, 1885; Schütt, 1887, 1895, 1896; Aurivillius, 1898; Entz, 1905.
Goniaulax polyedra Okamura, 1907.
non *Peridinium acuminatum* Ehrenberg, 1838.
non *G. acuminatum* var. *armatum* Schütt, 1895.

Cell polyhedral, in ventral view heptagonal, epitheca with 3, hypotheca with 2 corners. Apical pore elongate, directed to 1 side, transverse section nearly circular. Girdle equatorial, left-handed, with strong lists supported by spines. Theca strongly sculptured with pores. Intercalary bands narrow or broad. Cell contents brown. Plate formula 3′ or 4′.7″ 6*g*5‴ 3″″.

Distribution.—In all tropical and subtropical oceans, also littoral, and in slightly brackish water. Numerous. Rare in colder seas. In Australian waters on east coast only, from Eden, N.S.W., to Moreton Bay, Queensland; south coast of New Guinea.

GONIODOMA SPHAERICUM Murray & Whitting

Goniodoma sphaericum Murray & Whitting, 1899.

Spherical in form, with characteristics of the genus, diameter 35-50 μ. Autotrophic.

Distribution.—Mediterranean, Atlantic, and Indian Oceans. Southern Ocean west of King I. in west wind drift at temperature of 12.9°C.

Genus CERATOCORYS Stein

Ceratocorys Stein, 1883.

Body rounded or angular; epitheca and hypotheca often flattened distally: girdle in anterior $\frac{1}{3}$; well-developed fins; surface smooth or rugose, coarsely pitted, usually with fins and sheathed spines along sutures. Formula 3′ 1*a* 5″ 8*g* 6‴ 1*p*1″″. Fission plane oblique, skeleton retained. Chromatophores yellow or brown. Type species *C. horrida* Stein.

CERATOCORYS HORRIDA Stein

Fig. 242*a*, *b*

Ceratocorys horrida Stein, 1883.
C. tridentata von Daday, 1888.
C. spinifera Murray & Whitting, 1899.
C. horrida var. *longicornis* Lemmermann, 1899.
C. horrida var. *africana*, 1907.
Dinophysis jourdani Gourret, 1883.

Body more or less angular, more or less constricted sideways. Apical region angular, bluntly pyramidal, rarely somewhat rounded. Girdle lists very wide. Hypotheca with 5-10 long spines, 4 arising from the corners of the antapical plates, 1 in the left ventral list wing, the rest along the post-equatorial ridge. The spines are winged with a strong central axis from which small ribs project on all sides. Size and direction of spines very variable. Chromatophores yellow-brown.

Distribution.—Warm water in all oceans, also in coastal water. Numerous in the Mediterranean in summer. East Australia from New Guinea to Maria I., Tas. (August 1940), Eden (August 1938) and Montague I., N.S.W. (October 1938). Not found on west or south coasts of Australia except at one station south of Port Fairy, Vic.

CERATOCORYS ARMATA (Schütt) Kofoid

Fig. 243*a*, *b*

Ceratocorys armata (Schütt) Kofoid, 1910.
Goniodoma acuminatum var. *armatum* Schütt, 1895.
G. fimbriatum Murray & Whitting, 1899.
G. armatum (Schütt) Schmidt, 1901.
Goniaulax fimbriatum Schröder, 1906.

A large form with 3 or 4 short horns which arise from the rims or edges of the hypotheca plates and from the rear end of the left ventral list. Girdle lies in the upper ⅓ of the angular body; epitheca ½ as high as hypotheca. Apical and antapical region bent sharply towards ventral region. Girdle lists and ventral list much less developed than in *C. horridum*. Broad pore; free intercalary bands often present along sutures with low, toothed, smooth or ribbed lists. Numerous large pores present. Brown chromatophores.

Distribution.—An interoceanic warm-water form which may be carried by currents into subtropical and mixed regions; south-east Australian waters.

CERATOCORYS GOURRETI Paulsen

Fig. 244*a*, *b*

Ceratocorys gourreti Paulsen, 1930.
Ceratocorys jourdani (Gourret) Kofoid, 1910 partim.
Phalacroma jourdani Schütt, 1895; Entz, 1902, 1905.
Phalacroma ceratocorys Entz, 1902, 1905.
Ceratocorys horrida Stein, Murray & Whitting, 1899.

Habit of a *Phalacroma*. Body in side view rounded oval, more or less constricted at sides. Epitheca very low. In sagittal plane arise 5 winged spines, 2 ventral, 2 basal, and 1 more dorsal. Length (without spines) 85-95 μ.

Distribution.—A warm-water form in all oceans. Numerous in the Mediterranean in summer. Very rare on the east Australian coast, one example occurring off Trial Bay, N.S.W., in 1939, and several off Eden in 1952. Also numerous in the water of the west wind drift south of Port Fairy, Vic., 1952.

Genus OXYTOXUM Stein

Oxytoxum Stein, 1883.

Cell elongated, club-shaped to spindle-shaped: girdle deep and broad, anterior: hypotheca and/or epitheca often pointed: ventral area short, often reduced: no apical pore. Plate formula 5′ 5″′ 1″″. Theca with longitudinal or transverse ridges, often poroids. Type species *O. scolopax* Stein.

Oxytoxum is recorded from Low I. by Marshall (1934) but was rarely found in the present investigation, and then only on the east coast.

OXYTOXUM SCOLOPAX Stein

Fig. 245

Oxytoxum scolopax Stein, 1883.

Epitheca pyriform or consisting of a more or less rounded part below and a spine above. Hypotheca very long, somewhat bent, obliquely conical, antapical consisting of a bladder-shaped end piece with a spine. Theca with pores in longitudinal rows or striped. Intercalary lines often well marked.

Distribution.—Warm-water form, probably interoceanic. Also in Mediterranean. One example from the Carteret Group, Solomon Is.

OXYTOXUM TURBO Kofoid

Fig. 246

Oxytoxum turbo Kofoid, 1907.

Epitheca hemispherical with a short thick spinelet. Hypotheca long, swollen below girdle, pointed at base. Theca longitudinally striate, striations fine; *c.* 50 by 22 μ.

Distribution.—Tropical Pacific, off California (Kofoid), 1 example from eastern Australia.

OXYTOXUM DIPLOCONUS Stein

Fig. 247

Oxytoxum diploconus Stein, 1883.

Epitheca short and pointed with concave sides. Hypotheca long and pointed. Theca with numerous longitudinal ribs and pores. Length *c.* 60-160 μ.

Distribution.—Tropical Atlantic, Gulf Stream, Mediterranean. One example from Sydney Harbour.

OXYTOXUM sp.

Fig. 248

Epitheca obovate with a low apical swelling. Girdle narrow. Hypotheca swollen below girdle with 2 slight constrictions in lower ⅓. Antapex bluntly rounded with minute spinelet. Longitudinal lines intercepted by two transverse lines in hypotheca.

Distribution.—One example in a plankton tow off Jibbon Cape, Port Hacking, N.S.W., 21.vii.1943.

OXYTOXUM GIGAS Kofoid

Fig. 249

Oxytoxum gigas Kofoid, 1907.

Epitheca and hypotheca conical, sides at first concave, then straight, and then slightly convex. Apex terminating obliquely, bent dorsally. Antapex very pointed, body slightly constricted at sides. Longitudinal furrow very narrow on epitheca, deflected 1 width below the lower end of the girdle, which is displaced about 7 widths. Theca surface marked with parallel lines: 276 by 22 μ.

Distribution.—Tropical eastern Pacific. One station off Port Hacking 7.x.1943.

OXYTOXUM SUBULATUM Kofoid

Fig. 250

Oxytoxum subulatum, Kofoid, 1907.

A well-characterized species. The low, broad epitheca bears a long, cylindrical process, abruptly truncate above. Hypotheca like that of *O. sceptrum*. Girdle and sulcus deeply indented. Surface of hypotheca with 10-12 parallel longitudinal striae. 124-142 by 21-27 μ.

Distribution.—Tropical Pacific. East Australia: Trial Bay, N.S.W.

Genus PODOLAMPAS Stein

Podolampas Stein, 1883.

Cell somewhat pear-shaped, drawn out anteriorly to a more or less distinct apical horn ending in an apical pore. Girdle not apparent, probably fused with an adjacent precingular plate. Flagellar pore in ventral area: 2 strong apical spines support transverse wings, left wing being a combination of the left sulcal list. Plate formula (Kofoid) $2'' \ 1a \ 6'' \ 3''' \ 4''''$. Type species *P. bipes* Stein, 1883.

PODOLAMPAS BIPES Stein

Fig. 251*a*

Podolampas bipes Stein, 1883.
Parrocelia ovata Gourret, 1883.

Cell a broad pear-shape, narrowing to apical horn. Somewhat flattened dorsoventrally. Girdle not apparent, probably fused with adjacent precingular plates. Flagella pore in ventral area. Two strong equal antapical spines supporting transverse wings, the left being a continuation of the wing of the ventral area. Plate formula $2' \ 1a \ 6'' \ 3''' \ 4''''$. Theca porulate.

Distribution.—Tropical species, Atlantic, Pacific, and Indian Oceans, a guest in North Atlantic waters; Boeton Strait, Celebes; not infrequent on the east coast of Australia from Port Stephens, N.S.W., north, New Guinea and New Britain. Not found on west and south coasts.

PODOLAMPAS BIPES forma RETICULATA (Kofoid) Schiller
Fig. 251*b*

Podolampas bipes forma *reticulata* (Kofoid) Schiller, 1937.
Podolampas reticulata Kofoid, 1907.

Similar to type form but theca reticulate. Lower portions of antapical wings also reticulate near outer edge.

Distribution.—Two stations in eastern tropical Pacific and 1 station off Trial Bay, N.S.W.

PODOLAMPAS PALMIPES Stein
Fig. 252*a, b*

Podolampas palmipes Stein, 1883.

Cell elongated pear-shape, narrow in front, gradually tapering to a slender apical horn. Left antapical spine much longer than right, wings fused. Transverse seam often broad; 80-100 μ.

Distribution.—Interoceanic warm-water form, sometimes occurring as a guest in colder waters. Occurring rarely in east Australian waters from Moreton Bay, Queensland, to Port Hacking, N.S.W.

PODOLAMPAS sp.
Fig. 253

Cell pyriform, resembling *P. bipes.* Plate margins narrow, branching at sides, antapical spines resembling those of *P. palmipes,* but wings much narrower, continuous with those of ventral area.

Distribution.—One example from Jibbon Cape, Port Hacking, N.S.W., 11.vii.1949.

Genus CENTRODINIUM Kofoid
Fig. 254

Centrodinium Kofoid, 1907.

CENTRODINIUM sp.

A single example of *Centrodinium* occurred in plankton from eastern Australian waters (*Warreen* station 193/39). It is a robust form with a long, usually deflected apical horn (the plates had split), and an equally long, stout, ribbed antapical, somewhat twisted along the sutures and between them, and the plates and girdle are porulate. Plate formula, $2' \; 1a \; ? \; 5''$ or $6''$, $5''' \; 1p \; 4''''$.

As Böhm (1933) and Schiller (1937) stated, the genus is variable, and many of the species are doubtful. This form resembles Bohm's diagrams of *C. eminens,* but appears more robust and is possibly a new species.

Genus PYROCYSTIS Murray

Pyrocystis Murray, 1876.

Naked cell varying in form; hyaline with protoplasmic threads radiating from nucleus and attached to cell wall: only in reproductive phase are the spores dinoflagellate-like and spores of some species are not known (see Schiller 1937). Type species *P. pseudonoctiluca.*

PYROCYSTIS PSEUDONOCTILUCA W. Thompson

Fig. 255

Pyrocystis pseudonoctiluca W. Thompson, 1876.

P. noctiluca Murray, 1885; Blackman, 1902; Klebs, 1912; Pascher, 1937; Peters, 1930.

Cell spherical or somewhat elongated with thick cellulose membrane. Interior of cells is filled with liquid in which the protoplasm is present only as a thin wall coating which radiates from the nucleus and also contains small yellow chromatophores. In division, the protoplasm divides into 2 or 4 cells inside the separate cell membrane. The daughter cells behave as autospores and apparently grow to the size of the mother cell; 500-800 μ.

Distribution.—Warm water in all oceans. In Australian waters occurs between Babel I. (winter) and New Guinea, east to Lord Howe I. on the east coast, and between Rottnest I. and at least Cape Inscription on the west. Not recorded from the south coast.

PYROCYSTIS (DISSODINIUM) FUSIFORMIS (W. Thompson) Murray

Fig. 256*a*

Pyrocystis (Dissodinium) fusiformis (W. Thompson) Murray, 1885.

P. fusiformis forma *detruncata* Matzenauer, 1933..

Vegetative cells (cysts) of variable size, either thin, spindle-shaped or thicker and shorter with pointed or blunt ends. According to Matzenauer there are constrictions which appear as fine lines round the cell. He could not tell whether there is a partition membrane. He saw chromatophores in only 2 of the 4 parts so there are probably 4 separate chambers. Two size variations seem to occur—large cells (cysts) 600-1600 μ long by 255 μ and smaller cysts under 600 μ. The latter appear from Pavillard's work (1931) to produce *Gymnodinium* spores in ones or twos. The gymnodinians show the same form as Schütt shows for *P. lunula.* Their further fate is unknown.

Distribution.—Warm water. All oceans and adjacent seas. Rare in Australian tropical and subtropical waters.

PYROCYSTIS FUSIFORMIS forma BICONICA

Fig. 256*b*

Pyrocystis fusiformis forma *biconica* Kofoid, 1907.

Cell shorter and broader, with blunt rounded ends, sides straighter.

Distribution.—Pacific—California, east Australian coast from Jibbon Cape, N.S.W., to Sandy Cape, Queensland (winter form), New Guinea (summer form); west coast from Rottnest I. to Cape Inscription (winter form).

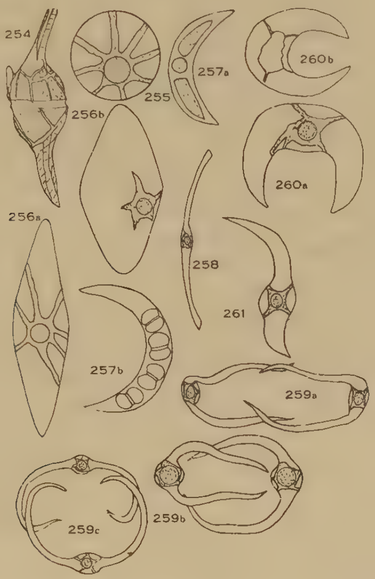


Fig. 254.—*Centrodinium* sp. Queensland coast. Fig. 255.—*Pyrocystis pseudonoctiluca* Thompson, 1876. Fig. 256.—*a*, *P. fusiformis* (W. Thompson) Murray, 1885; *b*, *P. fusiformis* forma *biconica* Kofoid, 1907. Fig. 257.—*P. lunula* Schütt, 1896. *a*, Normal form; *b*, with 4 gymnodinium spores. Jibbon Cape. Fig. 258.—*P. acuta* Kofoid, 1907. Port Hacking. Fig. 259.—*a*, *b*, *P. hamulus* Cleve, 1900. *a*, Port Hacking; *b*, Trial Bay; *c*, *P. hamulus* var. *semicircularis* Schröder, 1906. Port Hacking. Fig. 260.—*a*, *b*, *P. robusta* Kofoid, 1907. *a*, Jibbon Cape; *b*, east Tasmania (B.A.N.Z.A.R.E.). Fig. 261.—*P.* sp. Port Hacking.

PYROCYSTIS (DISSODINIUM) LUNULA Schütt
Fig. 257*a*, *b*

Pyrocystis (*Dissodinium*) *lunula* Schütt, 1896.
Gymnodinium lunula Schütt, 1895; Dogiel, 1906; Kofoid & Swezy, 1921.
Gymnodinium bicorne Kofoid & Swezy, 1921.
Diplodinium lunula Klebs, 1912.
Dissodinium lunula Pascher, 1916, 1927; Peters, 1930.

Two vegetative cyst forms are known. The primary cyst is a large, bladder-like, spherical cell with a diameter of 80-155 μ. In the thin membrane of dense accumulated plasma lies the nucleus in the middle of a plasma network from which numerous strands radiate, in which the chromatophores are to be found. In this, as in the huge fluid space inside the cyst, it resembles a cell of *P. pseudonoctiluca.* Inside this primary cyst 8-16 crescent-shaped independent cells, the secondary cysts, 104-130 μ long, are formed by succeeding divisions. These are free and float in the water, as do the primary cysts. The protoplasts of these sickle-shaped cells contract and form a *Gymnodinium* cell which rapidly divides to form 2, 4, or at most 8 swarm spores of *Gymnodinium* type. These break free from the cyst and become free-swimming. Their further fate is unknown.

Distribution.—Neritic and cosmopolitan, travelling with currents into brackish water. Lunula stage on Australian east coast from Maria I., Tas. (winter) to Moreton Bay, Queensland, and south of Port Fairy, Vic., in west wind drift, rare. Spherical stage common, New Guinea to Babel I.

PYROCYSTIS (DISSODINIUM) ACUTA Kofoid

Fig. 258

Pyrocystis (Dissodinium) acuta Kofoid, 1907.

Cell elongated, slender, straight to slightly curved, somewhat swollen in the centre and abruptly pointed at the tips. Length 13-21 times diameter of swollen mid region. Shape of ends and mid body separate this species from *P. lanceolata;* 615-1400 μ, diameter 45-95 μ.

Distribution.—Pacific, California (Kofoid), and New Guinea from a few stations.

PYROCYSTIS (DISSODINIUM) HAMULUS Cleve

Fig. 259*a*, *b*

Pyrocystis (Dissodinium) hamulus Cleve, 1900.

Cell body markedly swollen in the middle with 2 thin pointed horns, variously curved and often twisted, 250 by 40 μ.

Distribution.—Warm-water form. Rare in east Australian waters.

PYROCYSTIS HAMULUS var. SEMICIRCULARIS Schröder

Fig. 259*c*

Pyrocystis hamulus var. *semicircularis* Schröder, 1906.
P. semicircularis Kofoid, 1907.

Horns almost semicircular, long and slender with ellipsoidal mid body, often yoked in pairs, outline of complete and of long-horned single individuals almost circular or elliptical, mid body more convex on inner than outer side of arc. Horns tapering pointed, ends incurved sharply or sigmoid.

Distribution.—Warm-water form, east Australia: Port Hacking, N.S.W., to Sandy Cape, Queensland; mainly a winter form.

PYROCYSTIS (DISSODINIUM) ROBUSTA Kofoid

Fig. 260*a*, *b*

Pyrocystis (Dissodinium) robusta Kofoid, 1907.

A small robust species, deeply crescentic; differs from *P. lunula* in its greater curvature, stouter body, and absence of central expansion. Body fusiform, but bent into a deep crescent whose tips nearly meet or even overlap. Convex margin circular in outline. Greatest width at middle of body, tapering gradually to the tips.

Distribution.—Pacific, California, Australia: Port Hacking, N.S.W., off Cape Eddystone, Tas., 5.viii.1939, associated with other tropical species.

PYROCYSTIS sp.

Fig. 261

Form S-shaped with 1 blunt, short end and the other end much longer and more slender, tapering to a sharp point, both points being almost at right angles to the slightly swollen body. Nucleus held in protoplasmic web in swollen portion of body.

Distribution.—Port Hacking, N.S.W., 22.ix.42.

III. THE USE OF DINOFLAGELLATES AS INDICATORS OF WATER MOVEMENTS

It has been recognized by previous students of the group (e.g. Graham 1942) that some of the marine peridinians are useful in tracing the movements of oceanic water masses. While a number of species, e.g. *Peridinium oceanicum, Ceratium tripos*, etc., are cosmopolitan, others, e.g. *Ceratium cephalotum, C. euarcuatum*, etc., are restricted in their distribution. Graham and Bronikowsky (1944) agreed with Gran that temperature and not nutrients is the limiting factor. The author has studied the hydrological data collected by Mr. D. J. Rochford of this Division and finds very poor correlation of dinoflagellate occurrences with nutrients. It must be remembered in assessing the biological evidence in the light of hydrological data that organisms can exist for a time in an environment which has ceased to be favourable, but the presence of key organisms does indicate that, within a given time, the water mass in which they flourish has been close to the area in which they are actually found. The usefulness of these indicator forms increases with a decrease in their tolerance of unfavourable conditions. As an instance may be cited the results of a recent cruise in Bass Strait by F.R.V. *Derwent Hunter*. Miss P. Kott, of this Division, informed the author that *Thalia democratia* passed right through Bass Strait. Yet the warm-water *Ceratium* spp. and *Ceratocorys* did not pass west of Cape Everard, being replaced by the southern form *Ceratium horridum* as far as Port Fairy, Vic. where a mixture of *C. horridum* with *C. symmetricum* and *Ornithocercus quadratus* indicated another warm-water influence, differing from that east of Cape Everard. It would seem from this and from other instances that the dinoflagellates are more sensitive and therefore more valuable indicators than *Thalia democratica*. Another advantage which the dinoflagellates possess is that almost always two or more species or varieties are present to characterize a water mass, thus giving corroborative evidence although each form may be sparse. Most of the really good indicator species are present in very small numbers, so small that, in view of the large sampling errors inherent in plankton technique, statistical interpretation of the results is impossible. One must rely then on knowledge of the relative tolerance of the indicator forms derived from personal experience and from the evidence produced for these forms by others. In this example, the author checked his personal observations against the studies of Steemann Nielsen, Graham, Peters, and others, and the results are usually confirmatory. Dominant forms are rarely good indicators, except in estuarine or neritic influence. This is to be expected since, in unicellular organisms, the dominant forms usually gain their prominence by virtue of a certain degree of tolerance. A noted exception to this rule is the dominance of *Ceratium massiliense* forma *macroceroides* in Western Australian waters, but this instance suggests the existence of a closed system.

It will be noted in a study of the literature on dinoflagellate distribution that water masses are referred to in broad terms, rather than the restricted terms used by the hydrologist. Thus in the present work, no attempt is made to distinguish between the main body of the east Australian current and slope or eddy currents with the same biological characteristics. Such a differentiation could only be made if a very large number of stations had been regularly occupied. In the estuarine studies made in Port Hacking, tidal influence, wind, etc. confused the biological picture so that only the broadest analysis of the results was possible.

Frequently, cosmopolitan species, e.g. *Ceratium tripos, Peridinium ovatum,* etc., or species of wide distribution in water of certain characteristics, e.g. *Ceratium buceros* formae, *Dinophysis caudata,* and *D. tripos,* invade estuaries and become sufficiently modified for clones to be recognized as characteristic of an estuary or a limited estuarine region. For instance, *Dinophysis tripos* of south-east Australia can be distinguished by its form from *D. tripos* of south-east Tasmania: *Ceratium tripos* forma *pulchellum* has established itself in Port Phillip and Storm Bay and is not found at any appreciable distance from these estuaries. This estuarine clone can be distinguished from the oceanic form which occurs on the east coast of Australia.

There is also a vertical distribution of dinoflagellates, *Heterodinium* being restricted, according to Kofoid and Adamson (1933) to water below 80 m, while *Triposolenia,* and certain *Ceratium* species are also regarded as deep-water forms. Other species of *Ceratium, Peridinium,* etc. are physiologically adapted to surface water and are not found in deeper hauls.

IV. SEASONAL VARIATION AND FLUCTUATION IN SOUTH-EAST AUSTRALIA

(a) *Port Hacking*

In considering the Port Hacking-Jibbon phytoplankton, it is obvious that we are dealing with a mixture of estuarine and tropical-subtropical oceanic dinoflagellates in varying proportions, with a possible admixture at times of forms from the Tasmanian-Bass Strait region. Unfortunately, the indicator species for this last region is *C. horridum,* which was united with *C. buceros* by Jörgensen (1911) and separated by Schiller (1937), while *C. buceros* is, with *C. furca,* the predominant *Ceratium* in Port Hacking. *C. buceros* forma *denticulatum* appears to intergrade with *C. horridum,* and it is only by a study of the variation of *C. buceros* in Port Hacking that the identity of southern *C. horridum* can be determined. A continuous series of gradations between *C. buceros* forma *tenue,* forma *molle,* and forma *denticulatum* can be observed in the Port at times. *C. buceros* forma *claviger* and forma *inclinatum* are associated with oceanic species such as *C. carriense* and *C. massiliense,* so that they are regarded as oceanic, as are the more robust forms of *C. buceros* forma *tenue. C. tripos* and *C. pulchellum* are oceanic in Port Hacking and estuarine in Bass Strait-Tasmania. Intergrades of *C. macroceros* and *C. gallicum* can also be observed in Port Hacking.

It would appear that oceanic forms can invade estuaries in subtropical and warm-temperate regions and become endemic. In the earlier years of this study, *C. buceros* was estuarine, but later was largely replaced by a clone of *C. symmetricum* which first appeared as an oceanic form. The estuarine form in each case was smaller and more delicate than the oceanic one, and this applies also to clones of *C. gallicum, C. pavillardii,* and *C. trichoceros.* It is thus possible to decide when the species are estuarine and when oceanic by the delicacy of the theca, often by the size of the theca, and certainly by the length and strength of the horns. This is contrary to the finding of Steemann Nielsen (1934), who stated that the longer-horned forms of *Ceratium* occur nearer the coast.

Port Hacking is a drowned valley, with little admixture of fresh water except during heavy rains. The main part of the port is shallow, with deep water (10-15 m) at the heads of the arms. The water is marine in character, so oceanic forms are able to maintain themselves for a time and occur several miles up the estuary. At Audley, some 10 miles up, the main forms are estuarine, but oceanic forms such as *Goniodoma polyedricum* and *Ceratium falcatum* do occur there at times; usually, however, there is a paucity of dinoflagellates in the upper waters of Port Hacking. At Lillipilli, some 3 miles up, oceanic forms may be quite numerous. Such species are *Ornithocercus* spp., *Ceratium gravidum* (a shade species!), *Phalacroma* spp., *Ceratium massiliense, C. carriense,* and *C. pulchellum.* These occur during periods of easterly winds, especially in the winter. In the summer, the prevailing winds are north-east and south-east, so that the oceanic forms rarely penetrate far into the estuary.

Weekly plankton tows, using "Discovery" type N50 nets, were begun in August 1939 and were carried on until 1943, less regularly till discontinued after September 1945. They were resumed in October 1949 and terminated in October 1950. The earlier series of tows were made at a series of stations from Audley at the head of the port to 5-10 miles east of Jibbon Cape, the later tows were restricted to the Jibbon station and the seaward end of Port Hacking and Bate Bay.

1939.—In 1939, the plankton was almost entirely estuarine in character with comparatively few species represented. There was a peak of *Peridinium ovatum* in October, followed by inermis forms in November. The only oceanic representatives were *Peridinium crassipes, Pyrocystis pseudonoctiluca,* and *P. lunula.*

1940.—In 1940, the dinoflagellate population was small until April when Coral Sea influence was indicated by *Ceratium kofoidii* and southern influence by *C. horridum.* In May, *Peridinium globulus, P. quarnerense,* and *Ceratium vultur,* derived presumably from the Coral Sea, were mixed with indicators of the east Australian current, *C. gravidum, C. arietinum,* etc. *Ceratium dens,* regarded by Steemann Nielsen and others as an Indian Ocean-China Sea form, appeared in the plankton at this time. In June, the same facies was present with fewer species and numbers, while neritic forms of *Goniaulax, Peridinium,* and *Dinophysis,* e.g. *D. tripos, D. caudata,* and *D. okamurai,* were present. July showed *C. horridum,* the southern indicator with *Ornithocercus,* etc., indicating warm oceanic water. The spring months showed few forms with a slight outburst of *Dinophysis schroederi* and a few oceanic Dinophysidae, while, in the upper waters, a strong flowering of *Goniaulax polygramma* occurred.

There was no spring flowering of *Peridinium ovatum* in 1940.

1941.—As in 1940, there were few dinoflagellates until September. A peculiarity was the presence of *Goniodoma polyedricum* (an oceanic form) as far upstream as Audley in February. *Ceratium falcatiforme* and *Peridinium quarnerense* showed east Australian current and Coral Sea water respectively, in April. *Ornithocercus* spp. were present in July-August, with an influx of warm-water species in September, coinciding with an estuarine peak of *Peridinium conicum.* A spring maximum of *Goniaulax polygramma* and *P. ovatum* occurred in October-November with some oceanic influence.

1942.—This year the dinoflagellates suggest an onshore set of the east Australian current for the whole period except November, and the dinoflagellate flora was unusually rich in species and numbers. There was, for the first time, an upsurge of *Ceratium buceros* and *C. trichoceros* as estuarine forms, which lasted for 4 months. The maximum of

Peridinium ovatum occurred early, i.e. in September, and a *Goniaulax* peak did not occur. Among the warm-water oceanic forms, *Phalacroma* was unusually abundant. The occurrence of *Ceratium massiliense, C. carriense* forma *volans* and forma *hundhausenii*, and *C. extensum* forma *strictum* in the estuary, especially in January, was very unusual—these are all oceanic forms regarded as characterizing the east Australian current water mass. A large influx of *Peridinium* species, including *P. quarnerense* in February, shows Coral Sea influence, while in March the neritic *P. curtipes* was unusually abundant. *C. horridum* appeared off Jibbon in April as in 1940. An unusual May flowering of *Peridinium abei* occurred, while oceanic forms were rare until August, when Coral Sea and east Australian current forms were evident; these disappeared in September with an early *P. ovatum* flowering and reappeared in October (mainly Coral Sea forms) and December, together with an outburst of *Ceratium buceros.*

1943.—The outburst of *Ceratium buceros* observed in January 1942 was repeated in 1943, and peaks occurred of *Peridinium subinerme* in May-June, of *P. ovatum* in February and from August to November (unusually prolonged), and of *Dinophysis tripos* in November. There was no *Goniaulax* maximum. The picture is one of an estuarine flora with little incursion of oceanic water except between May and August, when tropical-subtropical oceanic species invaded the estuary. The influence of the Coral Sea water as indicated by *Peridinium globulus, P. quarnerense,* and *Ceratium vultur* was more evident than that of the east Australian current in May-June and August, but the forms indicative of the latter, e.g. *Ceratium gravidum, C. platycorne,* and *Pyrocystis robusta,* occurred also. *Ceratium horridum,* the indicator species for Bass Strait-Tasmanian water, was present in June and August.

1944.—In 1944, the plankton was poor in dinoflagellates, and there was no true peak of any form. Oceanic species were also scarce. *Ceratium pavillardii, C. vultur,* and *C. falcatiforme* indicated warm oceanic water in April-May and *Peridinium quarnerense* in June-August. *Goniaulax kofoidii* occurred in estuarine plankton for the first time in May of this year.

1945.—In this year, plankton tows ended in September as silk for nets was impossible to procure. The catches of peridinians had been poor, and only in April was there an indication of warm oceanic influence suggested by *Ceratium carriense* forma *hundhausenii, C. extensum* forma *strictum, C. karstenii,* and *C. massiliense.*

1949.—Tow nettings were resumed in May 1949. The plankton was rich in estuarine forms, notably *Ceratium buceros* forma *tenue* and forma *molle* and *C. furca.* The Coral Sea forms *Peridinium globulus* occurred in July-August and December and *P. quarnerense* in November-December. In July, the warm oceanic *C. pavillardii* and *C. teres* were also present.

The cold-water form *C. horridum* appeared in December. Apparently the usual warm oceanic influence was present from July to August and also from October to December, but peridinians were sparse. Among the estuarine forms, *Ceratium furca, C. fusus,* and *C. buceros* had peaks in May and December, an unusual feature, while the *Peridinium ovatum* peak lasted from September to December with a maximum in the latter month.

1950.—In 1950, more species of *Ceratium* were recorded than in 1948, but, once again, warm-water species were not numerous. Of the estuarine species, only *Peridinium curtipes* was ever numerous in the tows, in February, the first recorded major occurrence of this species since March 1943. The warm-water oceanic forms included *Ceratium falcatiforme, C. azoricum, C. pavillardii,* and *C. gravidum,* indicators of the east Australian current. There were no forms characteristic of the Coral Sea. The southern form *C. horridum* occurred in September.

(*b*) *Storm Bay, Tasmania*

Tow nettings with Discovery type N50 nets were made in Storm Bay in 1945, 1946, 1949, and 1950.

As would be expected in cooler waters, the number of species is much less than in Port Hacking, only some 41 species being represented. There is a characteristic autumn peak and a late spring-summer peak. One or other of these peaks may be absent—the late spring peak was apparently absent in 1945, and of longer duration in 1949 than in other years, while the autumn peak may have been absent in 1950. The sequence is much more regular than in Port Hacking and one sees the rhythmical picture of the temperate regions of the northern hemisphere which is so disorganized or lacking in the more northerly estuary.

Once again, *Ceratium buceros* is apparent as an estuarine form, but is accompanied by the southern forms of *Ceratium tripos* and *C. pulchellum* var. *eupulchellum* and var. *semipulchellum*. *Ceratium fusus, C. pavillardii* forma *delicatula, C. furca,* and the warm-water form *C. breve* also reach peaks in this estuary.

The presence of *C. lineatum* and *Peridinium pyriforme* suggests that water from the convergence may reach Storm Bay. This phenomenon is not recorded from the northern hemisphere. It is probably due to the very narrow continental shelf precluding the appearance of a truly neritic flora. In Australia, forms and species can only be regarded as oceanic-neritic, estuarine-neritic, estuarine, or oceanic.

In Storm Bay, the seasonal variation is more important than year to year fluctuations, in contradistinction to the situation at Port Hacking, where the reverse applies. This is due no doubt partially to the fact that the estuary is situated further south (i.e. nearer the convergence) and partly to the absence of any direct effect of the east Australian current on the system.

(*c*) *Continental Shelf*

The plankton collections from the south-eastern continental shelf show the same fluctuations as do those from Port Hacking. These collections were made with some breaks, from 1938 to 1945 and in 1947-1950, at first by F.R.V. *Warreen* and later by the use of fishing vessels running out from Coff's Harbour, Port Stephens, Port Hacking, Ulladulla, and Eden, N.S.W.

In 1938, the concentration of warm-water species occurred off the coast in winter and consisted of *Ceratium* species accompanied by *Phalacroma, Dinophysis,* and *Goniodoma;* the *Ceratium* continued into spring with *Ornithocercus quadratus, O. steinii, O. thurni,* and *Ceratocorys.* In May 1939, the warm-water forms occurred in late autumn and winter, but were rather sparse. *Amphisolenia,* rather rare on this coast, occurred in May and July. In 1940 there was a prolonged occurrence of warm-water species from April to June; in 1941 there was a small occurrence in autumn, the major occurrence appearing in spring and early summer: in 1942 tropical-subtropical forms were present through most of the year; in 1943 they appeared in winter with a few forms in autumn and spring; in 1944 in late autumn and winter; in 1945 only a few *Ceratium* spp. appeared in winter; in 1947 and 1948 in winter again, but in 1949 in autumn (few species) and 1950 from autumn to spring; in 1951 the forms appeared in winter.

(*d*) *The General Picture*

When the Port Hacking occurrences are compared with those on the continental shelf it appears that the following obtained:

1939. Oceanic forms did not penetrate the estuary.

1940. Oceanic forms were strongly represented in Port Hacking in autumn and winter.

1941. Few oceanic forms on the coast or in the estuary in autumn and winter with the penetration occurring in the spring.

1942. Warm-water oceanic forms reaching into Port Hacking throughout the year.

1943. Oceanic forms on the coast and in the estuary in winter.

1944. Estuarine influence predominated with some oceanic forms on the shelf in late autumn and winter.

1945. Poor dinoflagellate occurrences with slight oceanic influence on the shelf and in the estuary in late autumn and winter.

1949. Little oceanic influence in Port Hacking and on the shelf in autumn.

1950. A few oceanic species in Port Hacking and on the shelf from autumn to spring.

It is obvious from this summary of the movements of dinoflagellate species that the normal period when the east Australian current and its offshoots are nearest the south-east coast is in the winter, but that the influence of this current may appear earlier, when it is usually prolonged, or may be delayed until the spring. Further south, though catches there (Ulladulla, Eden, east Tasmania) are much less regular, the winter plankton catches seem to show the influence of Bass Strait water close along the coast, but from August to December tropical-subtropical forms appear at stations on the edge of the continental shelf, moving inshore as summer approaches.

It is interesting to note that, in discussing fluctuations in tunicate occurrences, Thompson (1948) recorded an unusual incursion of tropical and subtropical tunicates into south-east Australian waters in 1939 extending into 1940. This is shown by the dinoflagellates in autumn-winter of 1940, but not earlier. Unfortunately, the regular collection of zooplankton failed in 1941 and further correlations are impossible, except that tropical influence was shown by the peridinians in 1942, where Thompson recorded an influx of *Pyrosoma*.

The picture presented by the occurrences of dinoflagellates in Port Hacking is that of the appearance in the Port of indicator species derived from three external sources:

(1) The area delimited by New Guinea, the Solomon Is., and the east coast of Australia south of Lady Elliot I. to Trial Bay;

(2) The east Australian current, which appears from dinoflagellate indicators to approach the coast south of Trial Bay, and often south of Port Hacking, and frequently to mix with the Coral Sea water north of Port Hacking so that indicator species of both are represented (this Coral Sea plankton may represent the slope current);

(3) Water from the Tasmanian-Bass Strait region, which is poor in nutrients and unfortunately contains a sparse dinoflagellate (and diatom) population and must frequently remain undetected.

The maximum intensity of oceanic warm-water influence normally lasts for 3-4 months, usually between April and July or early August, but at times delayed or extending into the late spring. Variation in intensity of Coral Sea and east Australian current movements from year to year is suggested by the corresponding indicator species. The southern influence (*C. horridum*) occurs mainly in winter but may continue until December.

A noteworthy feature of the estuarine-neritic component is the change from year to year in the genera and species dominating the phytoplankton flowerings. In the earlier years *Goniaulax polygramma* and *Peridinium ovatum* were dominants in the blooms, but later (1942) *Ceratium buceros* and to a lesser extent *C. trichoceros* became important while *Goniaulax* took a minor role. In 1945, however, a new chain-forming species of *Goniaulax, G. conjuncta,* bloomed for a week and disappeared completely from the plankton as rapidly as it appeared.

Usually, the appearance of warm-oceanic indicator species is accompanied by the presence of a flora in which quantitative differences confirm the evidence of origin given by the indicators; e.g. Coral Sea indicators are usually accompanied by large numbers of *Peridinium* spp., while east Australian current water is accompanied by numbers of the Dinophysidae (comprising *Phalacroma, Ornithocercus,* and occasionally *Histioneis* and *Amphisolenia*), though neither on their own are specific enough to be regarded as indicators.

Study of the data shows that any seasonal variation is secondary in importance to major fluctuations. This is contrary to the experience of planktologists in the north European region of the northern hemisphere, where forms may be classified on their seasonal appearance. The same result is found if we take the number of species present, as a large number of species is usually accompanied by a large number of individuals of the dominant species.

It can be seen also that the oceanic dinophysids, e.g. *D. hastata, D. hindmarchii, Phalacroma, Amphisolenia, Ornithocercus,* become important when the species and numbers of *Ceratium* are also high, and that they are therefore useful indicators of the strength of the warm-water influence in Port Hacking.

Allen's (1941) statement that "in twenty years, no two years were alike, no two months were alike or no two weeks were alike" is certainly applicable to the Port Hacking results as can be seen from Table 1. His observation made at Scripps Institution that "no single species was ever able to hold the lead in production over a long period of time, rarely more than 10 days", is not altogether borne out in this estuary, where *Peridinium ovatum, Ceratium buceros,* etc. had peaks lasting for a month or more. However, these peaks usually comprise pulses with one major and one or more minor pulses representing a series of reproductive cycles at periodic intervals.

The occurrence of small, delicate forms of *C. buceros* and *C. trichoceros* in Port Hacking as endemic forms is interesting and is in line with the findings in regard to sedentary sublittoral forms in this region. Many of these are introduced forms which have also become endemic.

V. CHARACTERIZATION OF WATER MASSES IN THE AUSTRALIAN REGION BY DINOFLAGELLATES

In Australian waters, the most cosmopolitan genus is *Ceratium,* of which most species are oceanic. The estuarine species are *C. furca,* which replaces *C. hirundinella* as a brackish-water form, *C. fusus, C. buceros* forma *tenue* and forma *molle,* and more rarely *C. trichoceros, C. breve,* and *C. fusus*. In Victoria and Tasmania, *C. tripos* and *C. pulchellum* are estuarine while in more northerly waters they are oceanic-neritic. *C. buceros* is also oceanic, but there is a recognizable difference in form in each of these three genera between the oceanic and neritic representatives, the oceanic forms having longer apical horns. *C. symmetricum* is occasionally very numerous in estuaries, and appears to be replacing *C. buceros* in Port Hacking at the present time.

It would seem that, in the equatorial and Antarctic regions of the southern hemisphere, the dinoflagellate flora is reasonably constant throughout the year, as would be expected where temperature and salinity changes are minimal and do not exceed the tolerance of the indigenous flora. The characteristic feature of the south-western Pacific is the persistence of this constancy from the equator to the convergence and from the Antarctic to the convergence. Thus we can distinguish two external phytoplankton influences, tropical-subtropical and Antarctic. There is no record of an obvious oceanic warm-temperate flora in east Australian waters in Steemann Nielsen's studies or in those of the author.

(*a*) *Antarctic Dinoflagellates and Their Characteristics*

The indicator species for Antarctic water are *Dinophysis arctica, D. tuberculata, Peridinium turbinatum,* and *P. obovatum.* In addition, there is a wealth of *Peridinium* species, many of which, though eupelagic, have characteristic shapes in this region, e.g. *Peridinium depressum* (*P. antarctica* of Schimper), *P. piriforme,* and *P. breve.* The Antarctic peridiniums have dense cell contents, numerous chromatophores, large, rotund bodies, and a somewhat "uglier" shape than the forms of the same species found in Australian onshore waters. Schiller regarded them as specifically identical with their warm-water counterparts, and was probably correct in doing so. Paulsen (1949) considered Matzenauer's *P. sinaicum* from the tropical Indian Ocean to be identical with *P. cerasus* from the North Atlantic. Yet there are differences, difficult to describe, but obvious to the planktologist, between *P. cerasus* from the Antarctic and from the Australian estuaries.

It would be convenient to consider the Antarctic forms as separate species on ecological grounds, but, as the specific characters of the genus are limited, it seems impossible to do so. Paulsen has characterized *P. breve* and *P. piriforme* as "ugly", and the description is apt when one is familiar with Arctic or Antarctic plankton. Such a term is difficult to apply in practice, e.g. it cannot be used in a key, so must, it is feared, be abandoned.

Moreover, in certain areas, e.g. south-west of Western Australia, there appear intergrades between these Antarctic and the warm-temperate forms of the species so it seems we must be content to regard them merely as eco-forms. If we are to find new specific names for the warm-temperate, more streamlined *P. breve* and *P. piriforme*, then we must also find a new name for the rather rotund *P. crassipes* found by the author in the B.A.N.Z.A.R.E. plankton near the Antarctic mainland. For *P. crassipes* is considered by Paulsen and others to be a warm-water species. Similarly, *Dinophysis ovum* shows a stronger theca structure, and is larger than the *D. ovum* of Australian estuaries.

The only *Ceratium* species found in the B.A.N.Z.A.R.E. and Heard I. plankton are *C. pentagonum* forma *robustum* and (rarely) *C. lineatum*. The former is in the Antarctic apparently the counterpart of the latter in the Arctic.

Dinophysis ovum and the species of *Peridinium* occurring in the Antarctic as oceanic forms are nearly all estuarine-neritic in the warm Australian waters. This reversal of habitat towards the end of a range seems characteristic of many dinoflagellates, and has been observed also in many shore-line forms, both animal and algal.

(*b*) *Cool Temperate Region*

This is confined to the Tasmania-Bass Strait region, which appears to be a closed biological system with poor phytoplankton. The dinoflagellate indicator species (usually the sole dinoflagellate constituent) is *Ceratium horridum*. This species was recorded by Karsten (1906) from similar latitudes off the east coast of Africa. This region is also unusually low in nutrients, and the hydrological evidence agrees with that of the dinoflagellates.

(*c*) *Sub-Antarctic*

Sub-Antarctic water appears to be characterized by *Dinophysis truncata, Phalacroma pulchellum,* and *Ceratium petersii,* the last also recorded south of Cook Strait by Steemann Nielsen. *D. truncata* and *Ceratium lineatum* appear occasionally in south Tasmanian coastal waters, and *C. pentagonum* forma *robustum* in western Bass Strait at times, suggesting an occasional northward movement of sub-Antarctic water—probably diluted.

(*d*) *East Australian Current*

The east Australian current contains most of the *Ceratium* species recorded by Steeman Nielsen from the south equatorial current, together with the oceanic Dinophysidae, *Ceratocorys, Heterodinium* species, etc. which are associated with tropical and subtropical waters. *Peridinium* is relatively sparse. The ceratia are very long-horned and robust, discounting Steemann Nielsen's observation that long-horned forms appear nearer the coast with lower temperature.

The indicator species for this water are: *Ceratium azoricum, C. falcatiforme, C. gravidum, C. pavillardii, C. platycorne, Dinophysis fortii, Peridinium elegans,* and *Pyrocystis robusta.*

Steemann Nielsen's lists of the "Dana" expedition ceratia show a continuity from the south equatorial stream to the south-east coast of Australia (Gebiet III), and the number of species diminishes north-east of Eden where they are carried east to New Zealand by the west wind drift (Gebiet IV). The author's observations confirm this, and the continuity of the water mass from the south equatorial stream to the sub-Antarctic convergence south of Tasmania is also shown by the presence in the southern latitudes of *Heterodinium, Ornithocercus,* etc. Even the tropical genus *Histioneis* occurs as far south as Montague I. (36°S.).

(*e*) *Coral Sea*

There are significant differences between the flora of the east Australian current and that of the area north from Trial Bay to Lady Elliot I., thence to southern New Guinea and the Solomon Is. This has been designated by the author the Coral Sea region. It was sampled by the ill-fated F.R.V. *Fairwind* and by the Danish research vessel *Galathea* running from Port Moresby to Brisbane. The flora of the region is characterized by *Ceratium cephalotum, C. kofoidii, C. schmidtii, C. setaceum, C. vultur* forma *japonica* and forma *sumatrana, Ornithocercus steinii, Peridinium globulus, P. quarnerense, P. brochii, P. latispinum,* and *P. okamurai.* It is especially rich in *Peridinium* species which are much rarer in east Australian current waters. Occasionally *Ceratium dens,* regarded by other authors as an Indonesian form, appears in the Coral Sea. However, Pavillard (1935) recorded it from a station in long. 148°W. in the tropical Pacific. Its occurrence in the Pacific is so rare compared with that in the Indian Ocean and Indonesian waters that it seems probable that it is a "guest" on the east coast of Australia, indicating an admixture of water passing eastward through Torres Strait.

(*f*) *Features of East Coast Plankton Occurrences*

In this investigation, tropical-subtropical dinoflagellates have been found, especially in the spring and early summer, as far south as the sub-Antarctic convergence (lat. 44-45°S.). Frequently, between June and December, a tongue of cool-temperate water with *C. horridum* as its indicator moves northward to Sydney close to the coast. At such times, this species will be found on the continental shelf stations from Cape Pillar, Tas., to Port Hacking, N.S.W., in a plankton very poor in plant forms, while, farther east, in water 3-5°C warmer, will be found the east Australian current water with a relatively rich flora of warm-water *Ceratium* species and Dinophysidae.

Steemann Nielsen's records show that some 26 species of *Ceratium* occurred south of lat. 30°S., but not north of it. The author has confirmed this, and finds also that a number of species, mainly *Peridinium* spp., are characteristic of the more northerly water mass, which appears to flow southward along the continental shelf, possibly with the slope current, as far as Port Hacking in the winter or early spring. Usually, this water contains mixed Coral Sea and east Australian current elements, one or other predominating. At times, when strong easterly winds are frequent, the east Australian current dominates and its plankton elements are found in the estuaries. Unfortunately, there are not sufficient data to correlate these water movements with the seasons.

The Barrier Reef flora does not appear to contribute much to the other two southward-moving systems. It contains fewer species of *Ceratium* than occur in the other two regions and occasionally shows a few specimens characteristic of the Coral Sea—*C. schmidtii, C. kofoidii, Peridinium brochii,* and others. The most frequent forms are *C. breve, C. tripos* forma *tripodioides, C. massiliense, C. carriense,* and a characteristic form of *Dinophysis caudata.* The seasonal movement of water eastward through Torres Strait is evidenced by the occasional occurrence of *Ceratium dens* in the Coral Sea and, as far south on the Australian coast as Montague I.

The effect of the cool-temperate water along the south-east coast of New South Wales is shown by the neritic-estuarine occurrence of *Dinophysis tripos,* which is replaced by *D. caudata* north of that influence. The estuarine forms *D. schroederi, D. ovum,* and *D. okamurai* also peter out north of Port Hacking.

From lat. 34°S. northward, *Peridinium ventricum, P. abei, P. ovum,* and *P. okamurai* appear regularly in the estuaries. All these have been described from Mutsu Bay in northern Honshu, Japan, where they extend beyond the winter boundary of the subtropical convergence, i.e. they extend farther north than they do south.

The tropical neritic-estuarine *Dinophysis miles* has not so far been found on the east coast of Australia, though it does occur in Torres Strait, at Thursday I.

(*g*) *South Coast of Australia*

The cool-temperate Tasmania-Bass Strait region has already been considered, since its influence passes along the east coast. It would seem to be bounded on the west by a line from the west coast of Tasmania, east of Black Diamond, to Cape Otway. West of this, the flora is warm-temperate to subtropical and appears to be divisible into five subfloras:

(1) South Australian gulf flora, characterized by *Ceratium carriense, C. extensum, C. gallicum, C. symmetricum,* and *C. vultur,* none of which is recorded west of Port Lincoln or east of Cape Otway.

(2) Flora of the west wind drift. In May-July, and probably at other times, warm-water forms reach the west coast of Tasmania, mixing with the cool-temperate forms of western Bass Strait. The indicator forms found were *Ceratium platycorne, C. falcatiforme, C. axiale,* and

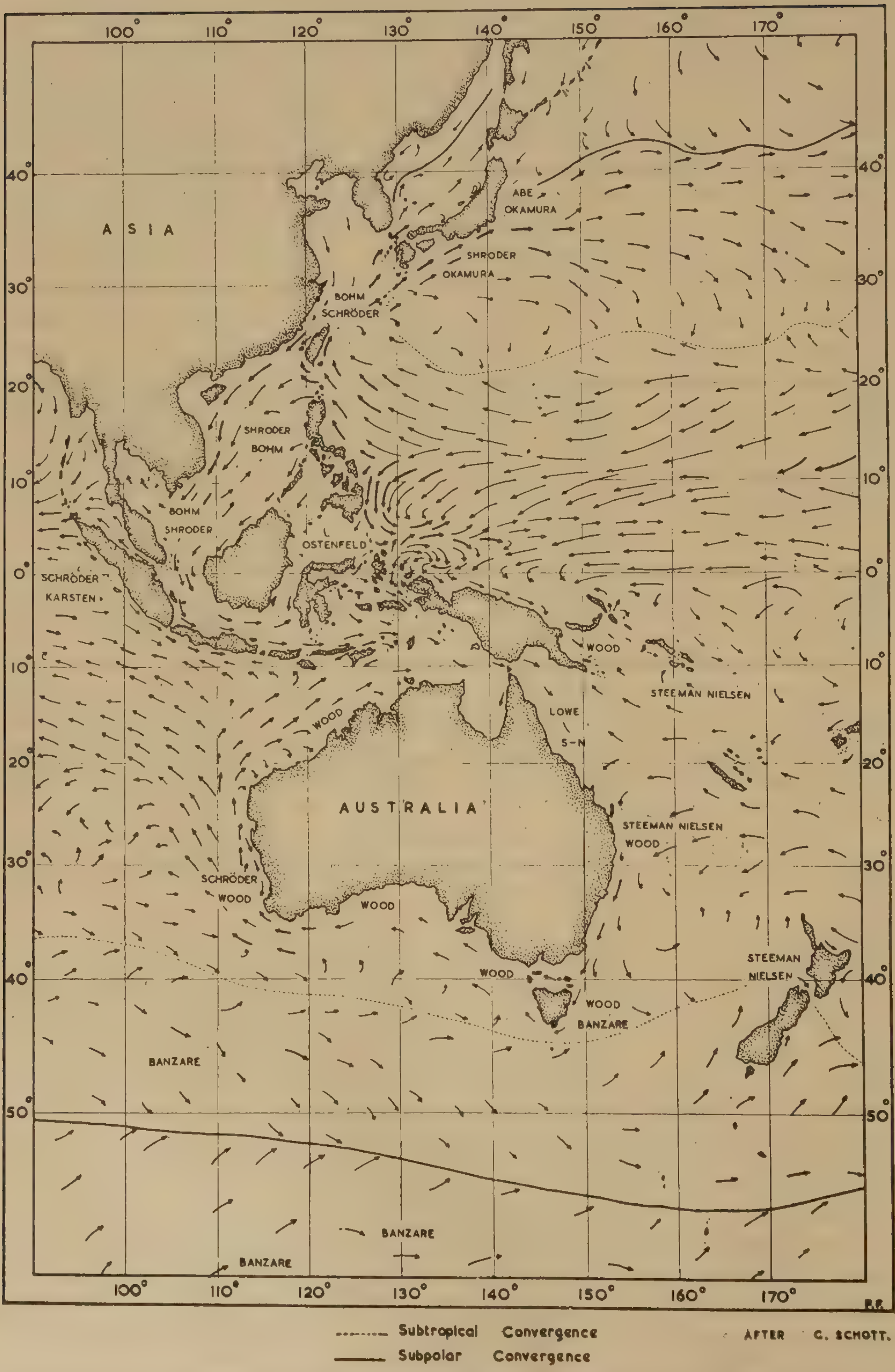

100°
110°
120°
130°
140°
150°
160°
170°
40°
30°
20°
10°
0°
50°
ASIA
ABE
OKAMURA
SHRODER
OKAMURA
BOHM
SCHRÖDER
SHRODER
BOHM
BOHM
SHRODER
OSTENFELD
SCHRÖDER
KARSTEN
WOOD
STEEMAN NIELSEN
LOWE
S-N
WOOD
AUSTRALIA
STEEMAN NIELSEN
WOOD
SCHRÖDER
WOOD
WOOD
WOOD
STEEMAN
NIELSEN
WOOD
BANZARE
BANZARE
BANZARE
BANZARE
P.F.
Subtropical Convergence
Subpolar Convergence
AFTER C. SCHOTT.

Fig. 262.—Ocean currents in the Australian region, February-March. (After Schott.)

Ornithocercus quadratus. It will be noted that these species are more tropical in origin than those occurring to the north-west (subflora 1), and there is a similarity with subflora 3 though the indicator species differ. In July 1952, vertical hauls in 720 m off Port Fairy, Vic., contained a large assemblage of tropical forms, including *Ceratocorys gourreti, Ceratium falcatiforme, Ceratium gravidum*, etc. The autochthonous nature of this flora was shown by the presence of a number of specimens of *Heterodinium*, including two species (*H. asymmetricum* and *H. scrippsae*) which, according to Kofoid and Adamson (1933) do not occur above 80 m. These specimens, especially as they were relatively numerous, preclude the possibility of the water sampled having passed through Bass Strait. Moreover, all samples taken farther east in Bass Strait showed typical *C. horridum* with *C. tripos* near Port Phillip. This confirms the findings of 1951, though the tropical nature of the flora was more marked in 1952.

(3) Albany-Israelite Bay flora, of which the indicators are *Ceratium falcatum, C. ranipes, C. teres, Ornithocercus magnificus, Pyrocystis pseudonoctiluca*. At times, this warm-water flora is found in Princess Charlotte Sound, but at other times it is found farther south with an inshore flora related to the west coast flora, and probably identical with subflora 4.

(4) The Great Australian Bight flora, which lacks *Ceratium teres, C. extensum, C. dens, C. karstenii*, and *C. arietinum*, but contains *C. massiliense* forma *macroceroides, C. lunula*, etc., mostly robust, long-horned forms. The area appears to be a biological sub-area containing a west coast, rather than a south coast flora. Captain Downie of this Division considers that Israelite Bay forms a recognizable dividing point for fishing. Unfortunately sampling was not frequent enough to allow of detailed correlation of dinoflagellates with water movements in the south of Australia.

(5) The south-west corner of Western Australia.—This subflora is a transition between the west coast flora and that of the Great Australian Bight, and contains *Ceratium lunula, C. macroceros, C. buceros, C. pulchellum, C. tripos*, and *C. trichoceros*, which differentiates it from the flora found to the east. *C. pulchellum* was not found on the west coast, and *C. tripos* was confined to the southern portion. The forms of *C. pulchellum* and *C. tripos* are similar to those of the cool-temperate Port Phillip while *C. macroceros* is usually considered a cool-temperate form. However, the other species, e.g. *C. massiliense, C. lunula*, etc., suggest warm-temperate water, so this is apparently a mixing with cool and warm elements.

It would appear that the tropical-subtropical current which reaches Albany continues eastward as the west wind drift (q.v.) to the west coast of Tasmania, where it meets the Bass Strait water indicated by *Ceratium horridum* and loses its identity, probably turning south-east and flowing to the south of Tasmania, then east again joining with the branch of the east Australian current flowing east from the vicinity of Eden (Fig. 263).

(*h*) *West Coast—Cape Naturaliste to Cape Inscription*

The dinoflagellate flora of the west coast is characterized by the numerical preponderance of *Ceratium massiliense* forma *macroceroides, Ceratium lunula,* and further north (Cape Inscription area) of *C. karstenii.* There are far fewer species of *Ceratium* on the west than on the east coast, and so far *Amphisolenia* is not recorded, while *Ceratocorys, Goniodoma, Podolampas,* etc. have been recorded only by Schröder from Hundhausen's material collected near Fremantle, but possibly at sea.

This phytoplankton is characteristic of temperate water in the fact that it is poor in species but contains great numbers. One does find blooms of *Ceratium massiliense* forma *macroceroides* and the diatom *Rhizosolenia castracanei* in numbers resembling Antarctic plankton catches. Blooms of these proportions have not been found in catches from other Australian waters except for the blooms of blue-green algae in New Guinea and the Solomon Is., nor are the blooms in other regions confined to a single species.

In the Swan River, W.A., *Dinophysis caudata* is found (not the cooler-water form *D. tripos*), the *Goniaulax* flora resembles that of Port Hacking except in the ratio of *G. spinifera* to *G. digitale, Peridinium abei* and the warm-water oceanic forms *P. quarnerense* and *P. globulus* occur in March. As these two forms are tolerant, they are probably derived from a warm-water mass offshore.

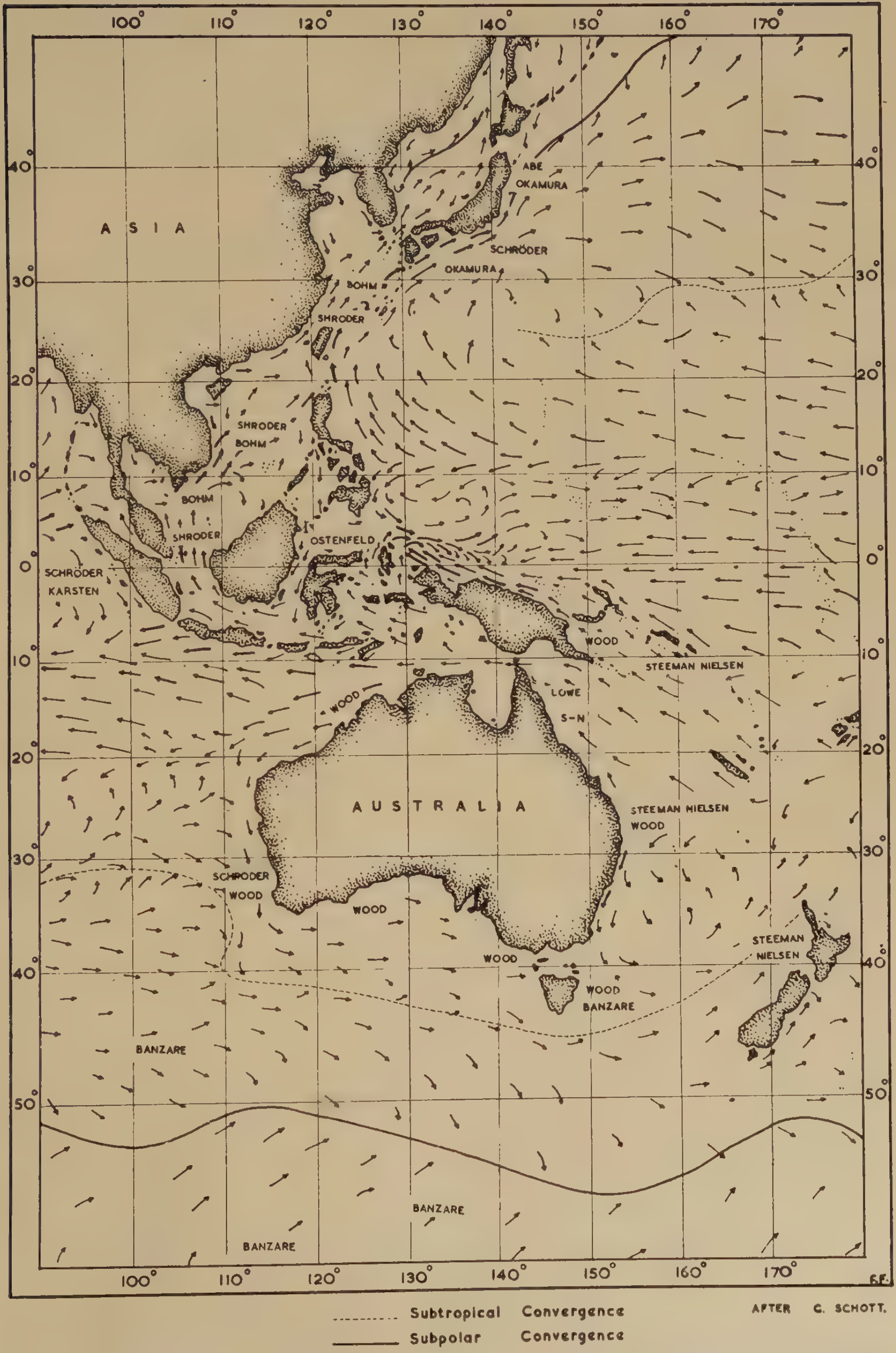
It would be seen that the *macroceroides* flora is part of a closed biological system, and there is other evidence that this is so.

(*i*) *North Australian Region*

Unfortunately, there are few phytoplankton samples available from the north coast of Australia. Those that have been examined show a flora which has much in common with that found by Schröder in Banka Strait and in the north-west Sunda Sea, and, apart from a smaller number of ceratia, with the flora of Boeton Strait (Ostenfeld 1915).

The dinoflagellate flora of northern New Guinea resembles that of the equatorial counter-current as described by Steemann Nielsen, as regards *Ceratium*; the tropical Dinophysidae are also well represented. To sum up:

(1) An Antarctic environment does not reach the south coast of Australia at any point, but a few stray Antarctic forms of eupelagic species suggest that there may be an occasional slight ingress of sub-Antarctic water mass into southern Tasmanian waters.


100°
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OKAMURA
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SHRODER
SCHRODER
KARSTEN
OSTENFELD
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BANZARE
BANZARE
BANZARE
BANZARE
E.F.
Subtropical Convergence
Subpolar Convergence
AFTER C. SCHOTT.

Fig. 263.—Ocean currents in the Australian region, August-September. (After Schott.)

(2) Apart from that, there appears to be a closed cool temperate area round Tasmania, extending across Bass Strait, and in the winter reaching northward to Eden and at times to Port Hacking (as evidenced by *Ceratium horridum*), flanked in the east by the east Australian current. In summer this eastern boundary moves west, at times as far as Wilson's Promontory. The western boundary lies to the east of Black Diamond and Port Fairy.

(3) Tropical water of the east Australian current, bearing a rich *Ceratium* flora with *Heterodinium, Histioneis,* and other tropical genera and species characteristic of the sub-equatorial current, reaches the coast of New South Wales between Trial Bay and Port Hacking, extending south to the northern edge of the convergence, i.e. about 48°S.

(4) The Coral Sea appears on available evidence to be characterized by a *Peridinium* flora and a sparser *Ceratium* component and to influence strongly coastal waters between Moreton Bay and Trial Bay, extending south to Sydney in the winter.

(5) The Barrier Reef region appears to have a different flora with still fewer *Ceratium* species, resembling the flora of Torres Strait and presumably the Arafura Sea. Some mixing with Coral Sea water is evidenced by the sporadic occurrence of Coral Sea forms.

(6) The north Australia, Coral Sea, and north-west Australian regions have a flora strongly resembling that which extends northward through Formosa Strait and the Kuro Shio current to Japan, characterized by *Peridinium abei, P. ovum, P. ventricum,* and *P. hirobis. Ceratium dens* is often associated with this flora.

(7) The west Australian coast has many fewer species than the east coasts of Australia and Africa, which have a great deal in common. The region between Shark Bay and Fremantle has an abundant growth of a few species, e.g. *C. karstenii, C. lunula,* and especially *C. massiliense* forma *macroceroides,* which resembles the abundant growth found in the Antarctic, and not found elsewhere in Australian coastal waters.

(8) The region between Cape Naturaliste and Israelite Bay is more subtropical in character with *Ornithocercus, Ceratium ranipes,* etc., but with some of the characteristics of the more northerly flora, e.g. *C. massiliense.* This flora possibly persists across the Great Australian Bight to Western Tasmania where it mixes with Bass Strait water or turns south to merge with the west wind drift.

(9) North of this, i.e. between Israelite Bay and Port Lincoln, is a rather ill-defined region, with fewer species and smaller concentrations than the western region.

(10) The South Australian gulf region characterized by *C. teres, C. extensum,* and the warm-water form of *C. pentagonum.*

The regions delimited by the dinoflagellates agree quite well with those of Hedley and Iredale. The Rossian includes the subantarctic flora,

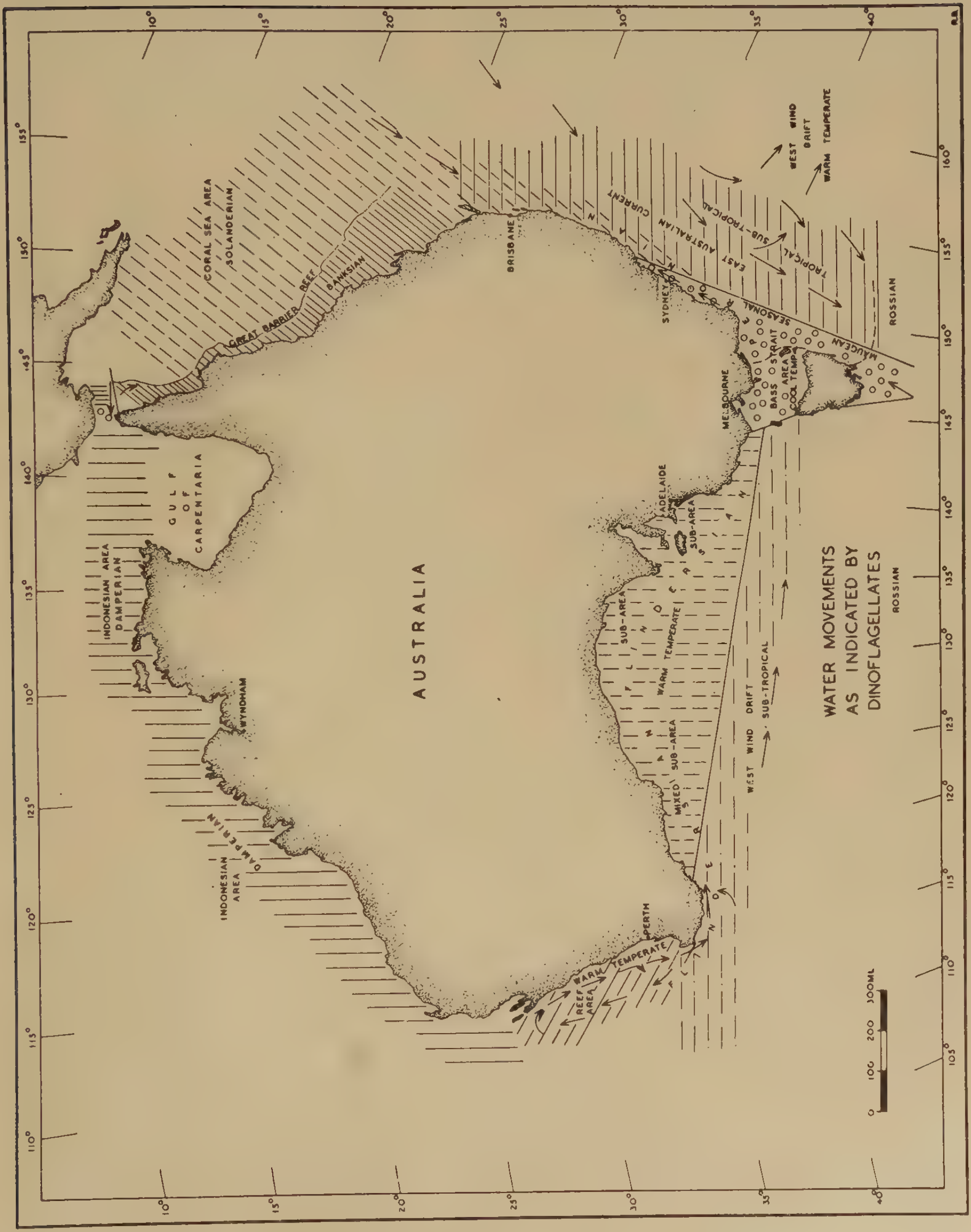
WATER MOVEMENTS
AS INDICATED BY
DINOFLAGELLATES
AUSTRALIA
CORAL SEA AREA
SOLANDERIAN
GREAT BARRIER REEF
BANKSIAN
BRISBANE
EAST AUSTRALIAN CURRENT
SUB-TROPICAL
TROPICAL
WEST WIND DRIFT
WARM TEMPERATE
SYDNEY
SEASONAL
BASS STRAIT
AREA
COOL TEMP.
MAUGEAN
ROSSIAN
MELBOURNE
ADELAIDE
SUB-AREA
WARM TEMPERATE
SUB-AREA
MIXED
SUB-AREA
WEST WIND DRIFT
SUB-TROPICAL
ROSSIAN
PERTH
WARM TEMPERATE
REEF AREA
INDONESIAN AREA
DAMPERIAN
WYNDHAM
INDONESIAN AREA
DAMPERIAN
GULF OF CARPENTARIA
10°
15°
20°
25°
30°
35°
40°
110°
115°
120°
125°
130°
135°
140°
145°
150°
155°
160°
0
100
200
300 ML

Fig. 264.—Ocean regions as demarcated by dinoflagellate associations.

Maugean, south and eastern Tasmania (cool temperate), the Peronian is divided into two and the author would put the southern boundary nearer Gabo I. than Wilson's Promontory in the winter; the Banksian is the area inside the Great Barrier Reef, the Solanderian is the Coral Sea region, the Damperian, the north Australian, about which we have insufficient data, but the Flindersian, a warm-temperate region, is characterized by several floras which have a great deal in common.

VI. The Role of Dinoflagellates in the Sea

As has been stated earlier, dinoflagellates may be holophytic, holozoic, or may adopt both methods of nutrition according to circumstances. Thus the role of these organisms in the sea may be either anabolic or katabolic. They do not represent the large source of regenerated phosphorus and other nutrients that the diatoms do. Their numbers are small in the Antarctic when compared with those of diatoms, though, in the tropics, dinoflagellates may, and often do, outnumber the latter. Pavillard's statement (1935), "*Prorocentrum micans,* provocateur occasionel d'eau rouge, *Ceratium tripos* (??) *C. furca, C. fusus, Peridinium divergens* (??), *P. depressum, Goniaulax polyedra, Dinophysis caudata* sont à peu près les seuls capables d'atteindre cà et là une proportion numerique assez forte pour jouer un rôle sensible comme "primary food" oceanique", is not strictly correct. Frequently, in tropical waters and in the western Australian region, *Ceratium* species are sufficiently numerous to be significant in the biomass, and in the estuaries *Peridinium ovatum, Diplopsalis lenticula, Ceratium buceros, Goniaulax digitale, G. polygramma,* and *Gymnodinium* species must be added. Whether the ceratia actually are used as food by many organisms is uncertain, but the peridiniums are so used by tintininids, salps, etc. and the author has found *Exuviaella marina* predominating in mullet stomachs on one occasion.

Some *Gymnodinium* and *Goniaulax* species, on the other hand, produce definite toxins which can and do poison fish and molluscs (Sommer *et al.* 1937) and these species may, by their rapid reproduction, deoxygenate the water to such an extent as to asphyxiate other organisms, causing serious pollution. The frequent pollution of the Lane Cove River in Sydney is ascribed to such mass killing by *Gymnodinium* sp. and a similar mass killing of fish in Port Phillip in 1949 coincided with, and was probably due to, a sudden flowering of *Gymnodinium* which was in such numbers as to colour the whole of the port, and cause the asphyxiation of the fish—whether by competition for oxygen or by mechanically clogging the gills was not determined. That these organisms do secrete a toxin is shown by the work of Whedon and others on mussel toxins in California. There are no recorded cases of shellfish toxicity from Australia.

A recent opinion on nutrition in the sea is that the major plant food is provided by microflagellates and blue-green algae, and that diatoms and dinoflagellates are relatively unimportant. The latter are certainly sparse in the estuarine muds and overlying waters which have been studied, and are outnumbered by *Euglena, Eutreptia,* the microflagellates, ciliates, and bacteria, except on rare occasions. The actual role of diatoms, dinoflagellates, and flagellates in warm waters must remain a matter of conjecture for the present.

VII. Correlation between Dinoflagellate Occurrences and Other Factors

An attempt was made to correlate dinoflagellate peaks in Port Hacking with the hydrological data. Correlation was reasonably good in some years between temperature curves and dinoflagellate peaks, but in other years it was poor. Allen (1928) also found the degree of correlation varied from year to year. Nitrate and phosphate analyses do not correlate at all well with dinoflagellate occurrences, but this is to be expected in warm waters where the phytoplankton never reaches great proportions, and nutrients are uniformly low, since there will never be a rapid uptake of nutrients from the water, nor a sudden release; therefore the values will always be minimal, and significant changes, if they occur, below analytical level. Gran (1912) and Graham (1942) have also observed that dinoflagellate occurrence is related to temperature and not to nutrients.

The fact that Allen and the author get correlation between σT and dinoflagellates in some years strongly suggests that salinity and temperature are factors in the development of peaks, and that there are other factors which predominate at times. Correlation was not improved by assuming that the blooms were started by the water reaching a critical temperature.

Wind direction is also a factor, neritic forms being more numerous in lower Port Hacking and Bate Bay when the prevailing winds are offshore, oceanic when they are onshore. Prolonged north-easterly winds in the summer, and easterly to south-easterly winds in winter bring the oceanic plankton into the estuaries. Prevailing westerlies carry this plankton offshore and bring down the estuarine forms. Droughts and heavy rains on land affect the occurrence of estuarine swarms, which correlate well with dry years. Compared with earlier years, the wet years 1949-50 yielded few dinoflagellates in Port Hacking.

It is possible, too, that there is rhythm in dinoflagellate occurrences. The accompanying graph (Fig. 265) shows a correlation of *Goniaulax digitale* with lunar phases, peaks of reproduction occurring at new moon in October and December 1950 and January 1951. These peaks were independent of temperature and rainfall. Not only were the numbers greater at these peaks, but active sporing with disruption of theca occurred at this time.

Peridinium ovatum usually has a spring maximum, but this fails to appear in some years, possibly owing to flood conditions.

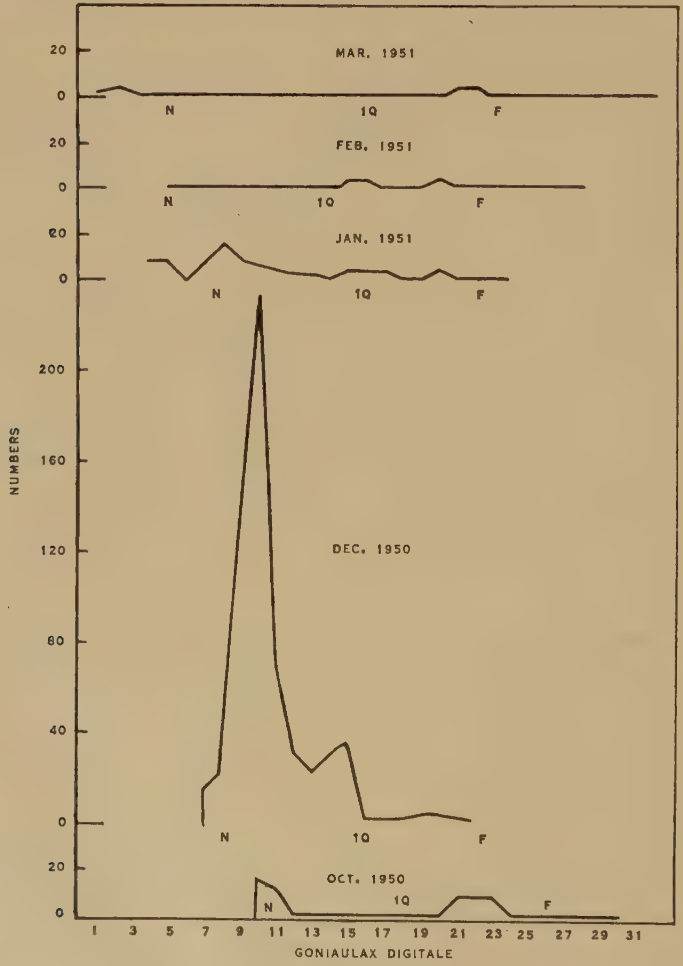

Fig. 265.—Correlation of *Goniaulax digitale* occurrences with lunar phases.

Sommer *et al.* (1937) found a similar periodicity in *Goniaulax catanella,* which reaches maximal numbers at the spring tides. In this example the organism contains a poison which is transferred to mussels, which become fatally toxic to human beings.

To sum up, no single factor or set of factors can be adduced to explain dinoflagellate maxima. The upsurging of such species as *Goniaulax* *conjuncta* (a species not recorded elsewhere), which reached dominance in Port Hacking for 7 days and then disappeared, is at present impossible to explain.

VIII. CONCLUSIONS

Thompson (1948) has adequately summarized the significance of plankton investigations on the east coast of Australia. His findings are related to tunicate occurrences, but apply equally well to dinoflagellates. He states (p. 173):

"It is therefore probably justifiable to consider the south-eastern Australian area as terminating naturally at about the commencement of the Barrier Reef area to the north" [the present author regards this as a closed tropical area]. "Since there is no evidence of a sub-Antarctic cold water influence being encountered towards the south, and since there is, towards the south, at most merely a gradual transition (marked by the dropping out of real circumtropical species and not by the intervention of typical cold-water species), no ostensible reason exists . . . for the placing of a southerly limit to the area, the general physical conditions of which probably persist to a point many miles to the south of Tasmania." The author, in general, agrees with this statement. *Amphisolenia* has not been found south of Port Hacking, but *Histioneis* persists at least to Montague I. and *Ornithocercus* and *Heterodinium* occur at times off the east coast of Tasmania. At least two of these genera are circumtropical. The tropical-subtropical peridinians appear to reach the convergence here as (from Steemann Nielsen's records) they do in New Zealand waters.

"It is now accepted that, in cold-water regions, the number of different species per genus to be found is very much restricted, though the total quantities are usually great, while in warm-water regions there is a great diversity of species, not usually occurring, however, in great quantities." One has only to examine the "pea soup" B.A.N.Z.A.R.E. phytoplankton catches and compare them with the collections made from the east coast by F.R.V. *Warreen* to see that this statement is true for the phytoplankton of the east coast of Australia. In the dinoflagellates, however, the position is different. There are fewer species in the Antarctic, but the numbers are only moderate, the bulk of the phytoplankton being made up of diatoms. In the warmer waters there are large assemblages of species and, at times, dinoflagellates outnumber diatoms, though they rarely form a very large part of the biomass.

Further, the predominant dinoflagellates in the Antarctic belong to the genus *Peridinium,* except for occasional outbursts of *Ceratium pentagonum* forma *robustum* and *Dinophysis.* In the warm waters, *Peridinium* becomes predominantly estuarine and neritic with a few oceanic species, *P. grande, P. murrayi, P. globulus, P. quarnerense, P. brochii,* etc., while *Ceratium* becomes the main genus as regards quantity and numbers of species, though in the Coral Sea, the oceanic *Peridinium* species are predominant in the catches—mainly *P. globulus* and *P. quarnerense.* The Dinophysidae are never dominant in oceanic catches in Australian waters, though on occasion a number of species are present in catches. If rare genera such as *Histioneis* or *Amphisolenia* are present, the other more common genera will usually be comparatively abundant.

"The probability that the Australian region has a greater affinity with the above-mentioned regions in the west Pacific than with the Californian region in the east Pacific is also suggested . . ." This affinity with the west Pacific, probably due to west-east water movement through Torres Strait, is shown by the species such as *Peridinium abei, P. ventricum, P. nipponicum, P. okamurai, Dinophysis okamurai, Ceratium dens,* and *C. schmidtii,* but the oceanic species of *Histioneis, Goniaulax,* and *Ceratium* have much in common with the flora described from the Californian region by Kofoid and his coworkers.

Thompson uses evidence from the tunicate occurrences to predict the type of fishery likely to be found in east Australian waters. Unfortunately, it has not been possible to correlate the evidence given by the dinoflagellates on the movement of tropical and cool-temperate waters and on the mixing of estuarine and oceanic waters of east Australia with pelagic fish occurrences, owing to the lack of accurate knowledge of the magnitude of these occurrences. One would expect that these fish movements would be related to water movements and it has been shown in the section devoted to the Port Hacking dinoflagellates that these organisms do give us considerable information concerning the nature of our coastal waters. Moreover, once the ecological significance of the dinoflagellate species is known, information on the water movements is immediately available from the catches. Thus the dinoflagellates should be of the greatest value in studying the movements of pelagic fish.

One significant fact emerges. Of the two genera *Heterodinium* and *Triposolenia,* which are benthic genera, the latter has not been recorded at all, while only a few examples of *Heterodinium* have been found. This suggests that little water from the middle or lower layers of the ocean is present on or near the continental shelf in Australian waters.

So far we have been considering the evidence on the east coast. On the north we have, of course, tropical species, but the stations are too few to give us much information.

On the west, we have evidence of a closed biological area inside the reef which extends up the coast of Western Australia, bounded by tropical water which moves southward well offshore and then eastward south of Albany, and, also straight across beyond the continental shelf of the Great Australian Bight to the west coast of Tasmania where it mixes with the water of the closed area of the Tasmania-Bass Strait region. The last-mentioned acts as a barrier between the east and the west, a barrier shown also by the euphausids, the intertidal fauna, and the algal flora (e.g. the distribution of *Macrocystis pyrifera*). The pelagic tunicates did not give any evidence concerning this closed area or the movement up the east coast of water therefrom, except for the petering out of some tropical tunicates in the region which dinoflagellates show is influenced by this water.

On the south coast, north of the tropical-subtropical west-east current, is another warm-temperate area, linked round Cape Leeuwin with the closed area of the west and resembling it in many ways. The shallow gulfs of South Australia have their own peculiarities which extend to waters round Kangaroo I. and east to Cape Northumberland.

The existence of a warm-water west-east current (west wind drift) would account for the non-appearance in the Great Australian Bight of any forms which characterize the Antarctic or the convergence.

The presence of numerically large concentrations of diatoms and dinoflagellates from Geraldton to Safety Bay and across the Bight may be correlated with the more rapid growth of *Arripis truttae* in the west than in the east.

The absence in the south and west of a number of species which are common in the east is paralleled in the tunicates.

IX. ACKNOWLEDGMENTS

The author wishes to thank those mentioned in the Introduction who assisted him by supplying material. Thanks are also due to Dr. H. Thompson for encouragement, to Professor T. Braarud for reading the manuscript and making useful suggestions, and to Mr. R. Breach, of this Division, for sterling assistance in the preparation of the diagrams for publication.

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THE BIOLOGY, MIGRATION, AND GROWTH RATE OF THE SCHOOL SHARK, *GALEORHINUS AUSTRALIS* (MACLEAY) (CARCHARHANIDAE) IN SOUTH-EASTERN AUSTRALIAN WATERS

By A. M. Olsen*

(*Manuscript received November* 30, 1953)

Summary

The school shark fishery in south-eastern Australian waters has operated on a homogeneous stock which has a low reproductive potential. The species is slow-growing; the smallest mature males (120 cm) are over 8 yr of age and the smallest mature females (135 cm) are at least 2 yr older. The gestation period is approximately 6 months and it is estimated that only about half the female population bear young each year.

Each gravid female carries 17-41 young with a mean number of 28. The lengths of the normal full-term embryos range from 280 to 350 mm with a mean for both sexes of 300 mm. The larger females tend to have the longest embryos. Slightly more male than female young (54 : 46) are born.

Because the inshore populations of juveniles have been dwindling and the size of the older stock is decreasing, it is believed that this slow-growing species is being overfished. Measures aimed at protecting school sharks in their vulnerable stages have been proposed. Any conservation programme will be long-term as this shark has such a low reproductive capacity.

I. INTRODUCTION

This investigation was commenced late in 1946 at the request of the Victorian and Tasmanian Governments, who were concerned about the falling catch of sharks from inshore areas and the future prospects of this fishery, which ranks third in importance in both States.

Australia became dependent on its well-organized edible school shark fishery for the supply of high potency vitamin A oils during the Second World War when hostilities cut off the overseas supplies of fish liver oils. Davies and Field (1937) and Jowett and Davies (1938) had shown that the liver of this shark species yielded half its weight of an oil high in vitamin A potency. As a consequence of both the increased demand for oil and the necessity for higher food production, the fishery was considerably expanded. Prior to 1941 only Victorian fishermen caught sharks commercially, but by the following year fishermen from Tasmania, South Australia, and New South Wales had entered this fishery. They followed the methods used in Victoria and within 4 yr had considerably reduced the number of adult sharks available in inshore waters.

This decline caused the various fishermen's organizations to approach their respective governments for an inquiry into the industry. However, the increasing demand for the flesh for the fresh fish trade had induced

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* Division of Fisheries, C.S.I.R.O., Hobart, Tas.

the more progressive fishermen to build and equip larger and more suitable craft, 40-50 ft in length, specially for long-lining within the waters of the continental shelf. As a result of the efficiency of these larger craft and the discovery of new fishing grounds in off-shore waters, the decline in the total catch of sharks in Victoria and Tasmania was temporarily arrested by 1945, and in the following year the catch showed an increase. From this improvement in the total catch it was inferred that the fishery had been stabilized. Its method had changed from a sheltered inshore to a hazardous off-shore operation which showed increased catches until in 1950 the total landed catch reached a maximum of 4,000,000 lb. Since that year it has fallen sharply to 2,500,000 lb. The widely ranging larger boats now have no new areas for exploitation.

II. Description and Distribution of the Species

The genus *Galeorhinus* Blainville has a wide distribution. The cosmopolitan species *G. galeus* (Linnaeus) ranges from the North and South Atlantic Oceans around South Africa into the Indian Ocean. *G. zyopterus* Jordan and Gilbert is found within the Pacific continental shelf of North and South America from British Columbia in the north to Chile in the south. The large *G. japanicus* (Müller and Henle) occurs in the Formosa-Japan area and has been reported from Amboina. In Australian and New Zealand waters the genus is represented by the smaller *G. australis* (Macleay 1881).

The naming of the latter species is in accordance with Fowler (1941), who recorded a complete bibliography of the synonyms for *Galeorhinus australis* (Macleay), the school shark of south-eastern Australian waters.

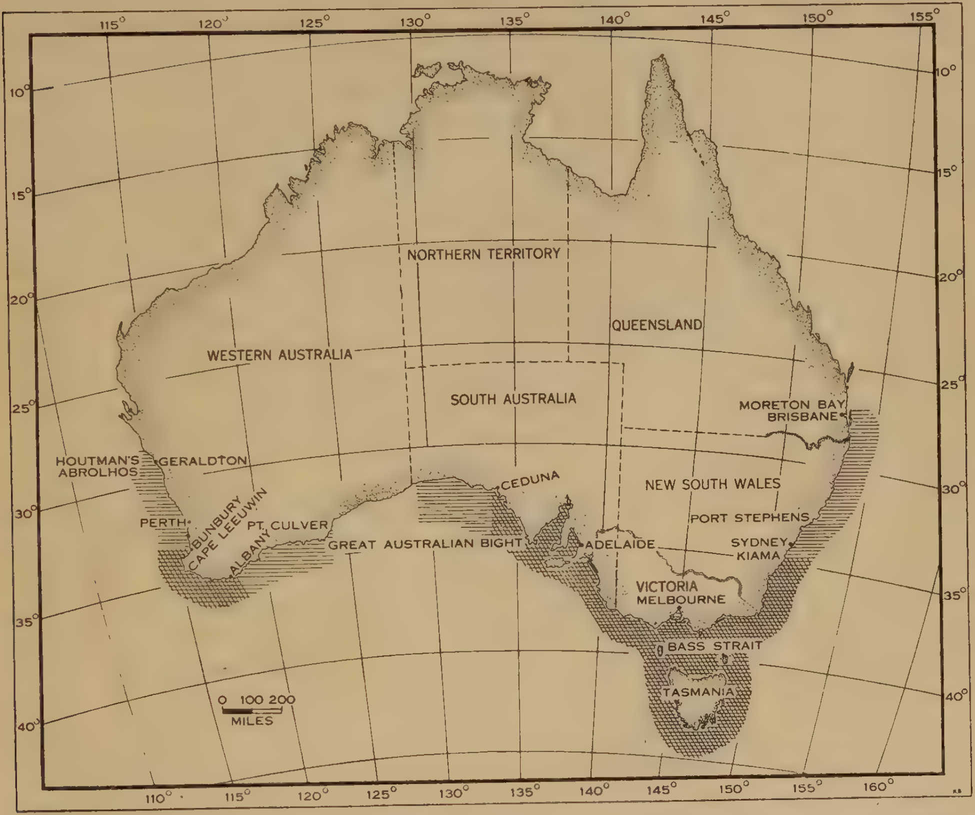
The school shark has a moderately long slender body, the snout is long and depressed, and the nostrils are much nearer the mouth than the snout. The mouth is crescentic; the small teeth, which lie in several rows, are alike in both jaws, being strongly notched and coarsely serrated on the outer side. A nictitating membrane is present and a small spiracle lies immediately behind the eye.

The gill openings are subequal; the fourth is widest and the fifth, located above the base of the pectoral, smallest. The scales are tricarinate, with three short points, of which the median is the longest.

The first dorsal fin is equidistant from the anterior bases of the pectoral and ventral fins. The second dorsal is small and begins slightly in front of the origin of the anal. The heterocercal caudal fin comprises one-fifth of the total body length and is longer than the head.

The upper body colour ranges from light bronze through to a slate grey, and the under surface is whitish. There is a correlation between the type of bottom and the colouring of the school shark, for dark-coloured sharks have come off rock bottoms, the bronze off sand. They are reputed to grow to a length of over 6 ft and to a weight of about 170 lb though there are no authentic records of this length and weight. The largest school shark caught by the research vessel measured 170 cm (5 ft 8 in.).

The earliest figure of the school shark, that of McCoy (1882), is inaccurate in many respects. McCulloch (1921) has an excellent figure of an adult male 152.5 cm long taken by a steam trawler in New South Wales waters.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WESTERN AUSTRALIA
SOUTH AUSTRALIA
MORETON BAY
BRISBANE
HOUTMAN'S ABROLHOS
GERALDTON
CEDUNA
NEW SOUTH WALES
PERTH
BUNBURY
CAPE LEEUWIN
ALBANY
PT. CULVER
GREAT AUSTRALIAN BIGHT
ADELAIDE
PORT STEPHENS
SYDNEY
KIAMA
VICTORIA
MELBOURNE
BASS STRAIT
TASMANIA
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MILES
110°
115°
120°
125°
130°
135°
140°
145°
150°
155°
160°

Fig. 1.—Distribution of the species and limits of the existing school shark fishery.

Distribution

G. australis has been found from Port Stephens south along the coasts of New South Wales, Victoria, and Tasmania, and through Bass Strait as far west in South Australia as lat. 32° 36′ S., long. 129° 54′ E. (22 fm) at the head of the Great Australian Bight (Waite and McCulloch 1915). Ogilby (1908) identified two of these sharks from Moreton Bay, Qld., and indicated that their occurrence was rare so far north.

In Western Australia it is found from Houtman's Abrolhos south to Cape Leeuwin and thence eastwards as far as Point Culver (F.R.V. *Warreen*). There is a 400-mile gap between Point Culver and the head of the Bight from which there are no records but there is no reason to assume that school sharks do not occur there. In Figure 1 the known distribution of the species and the limits of the existing fishery are indicated.

G. australis has been recorded also from Lord Howe I., New Zealand, and the Chatham Is. (Young 1929) 500 miles further eastwards.

III. THE FISHERY

(*a*) *History*

Records of the existence of a shark fishery in the early days of the settlement of Australia are very meagre. Except for the mention of the occasional practice of rendering the liver for oil, there is no record of any fishery prior to 1880. Tenison-Woods (1882) reported that sharks were caught off Recherche and Southport in southern Tasmania for their livers and fins, which were processed. Oil from the liver was extracted by boiling in open kettles; the fins were air-dried and bundled for export to the Chinese market. After the decline of this dried fin market, school sharks were often caught by the boat load for manuring apple orchards as they were very plentiful inshore around the Tasmanian coast (Bluett, personal communication). Although there were no records of shark being caught for the sale of the flesh, they were and still are important sources of bait for crayfish pots (traps).

Victoria was the first State to record shark in its catch statistics. In 1927, a 4-ton catch of school shark from Port Albert was entered in the catch records and from that date the recorded Victorian catch has risen steadily to the total of approx. 2,000,000 lb annually. By the early 1930's fishermen from various ports along the Victorian coast were catching sharks to supply the gradually rising public demand for fresh shark fillets. It was sold under the name of "flake". Tasmanian and South Australian fishermen did not engage in the commercial shark fishery until the early years of the Second World War. In New South Wales the main supply of shark, very little of which is school shark, comes from the catch of steam trawlers operating along that coast. A small shark fishery has been carried on in recent years around the south-western corner of Western Australia.

(*b*) *Methods of Capture*

In Australia school sharks are taken by long-lining. Mesh nets have not proved successful because of the tides. Initially all lines were hand-hauled but as the fishery moved further off shore more gear was used and mechanical hauling was adopted generally by about 1945.

The usual type of long line used is made up from $\frac{3}{4}$-1 in. sisal ground line with hooks on cotton or hemp "snoods" 3-4 ft long knotted to the main line every $2\frac{1}{2}$-4 fm. The distance between snoods depends on the preference of each individual fisherman though 3 fm is mostly favoured. Each snood is attached to the main line by a clove hitch, the knotted free end of which is passed through the lay of the line. Generally the free-board of the vessel determines the length of the cotton snood. It is a common practice to attach about 6-9 in. of 14-gauge galvanized wire to the hook and fasten the snood to an eye in the other end. Unless wire is used the sharp teeth of the shark cut the cotton line and it escapes. The sizes of the hooks vary from No. 9 to No. 12 ("Mustad") depending on individual preferences, the offset type being used also.

For convenience lines are made up into boxes of 80-100 hooks, and a "fleet" of lines consists of a varying number of boxes of lines capable of being knotted end to end.

Shark fishermen so arrange their departure from their home port that the setting of the long line starts about daybreak. Their complete trips vary from 12 to 36 hr. Lines are baited on the outward journey. The bait used consists of fish in plentiful supply, preference being for fresh Australian "salmon" (*Arripis trutta* Bloch and Schneider), barracouta (*Thyrsites atun* Euphrasen) or mullet (Mugilidae), salted bait being used only when fresh bait is unavailable. It has been found that fresh bait is always more successful.

In setting the long line a flag marker buoy, with or without a drum buoy attached, is thrown overboard and the requisite length of buoy line paid out. Depths fished for school sharks range down to 300 fm, i.e. down the slope of the continental shelf. Generally the buoy line and baited long line are joined together and a few fathoms of smaller diameter rope from the anchor is knotted to them. Should the anchor become fouled, the smaller line breaks, allowing the main line to be hauled. At the end of the set of gear there is the same arrangement of lines to an anchor and buoys.

The lines may be in one continuous set or several smaller "fleets" may be used. The actual number of boxes of hooks used each time depends on such circumstances as weather, tides, and type of bottom. Port Albert (Vic.) shark vessels have always carried the greatest number of hooks, the average lying between 2000-2500 hooks per boat.

IV. Biology

(*a*) *Collection of Material*

Practically all material for this study was collected during actual fishing operations conducted from either fishing or research vessels.

Tagging of sharks was the primary consideration though in most areas representative numbers of the catch were retained for dissection. In the inshore areas nets and handlines were used either separately or together and in every instance it was possible to catch sharks by either method. In some bays (George Bay) mesh nets ($2\frac{3}{4}$-$4\frac{1}{2}$ in. stretched mesh size) yielded best results whereas handlines gave better results in other areas (Pittwater). There was no apparent selective action of gear on sizes caught, since the sharks caught by either method of fishing ranged in size from recently born pups to gravid females.

Throughout this paper reference is made to particular estuaries in which most of the work was carried out. These localities were selected for the availability of material and are shown in Figures 13 and 14. They were representative of the area and most suitable for regular sampling. In all localities professional fishermen assisted with the work.

The method of tagging and equipment used for measuring the sharks have been described (Olsen 1953). Weights of very small, recently born juveniles were obtained on metric spring scales; otherwise, all weighings were obtained on clock-face spring balances weighing to either 30 or 100 lb.

Dissections were usually carried out immediately a haul was finished and all dressed (cleaned) weights were taken from carcases prepared by customary methods.

Throughout this paper the term "population" has been used to describe only that part of the stock present in a specified area.

(*b*) *Food*

The stomach contents of 600 school sharks of all sizes from over the greater extent of the fishery have been examined. It was found that 444 of the stomachs contained food; 438 yielded remains which, though in an advanced state of digestion, could be identified, and in six the digestion was advanced too far for recognition. The stomach contents showed that school sharks had a marked preference for fish and cephalopods (octopus and squid): 92 per cent. of the stomachs counted had either or both present. Food which had passed through the pyloric valve was unrecognizable.

Counts of the sharks with food in their gut caught in the open sea showed that they were foragers, for 98 per cent. of the stomachs contained freshly caught fish and cephalopods. The remaining 2 per cent. of the food was made up of the soft-shelled stages of the spiny lobster, *Jasus lalandii* (Milne-Edwards).

Seventeen species of fish have been identified from the stomachs of school sharks, the predominant ones being barracouta (*Thyrsites atun*) and jack mackerel (*Trachurus novae-zelandiae* Richardson). These two pelagic species apparently frequent the bottom zones at certain times of the year and are then preyed upon by sharks. The other species of fish found in the gut were nearly all bottom feeders and often restricted to reef conditions.

Only twice have elasmobranchs been found in the stomach contents. On both occasions the school sharks were trawled and it was not certain whether the small batoids (*Urolophus* spp. and *Raia australis* Macleay) were accidentally swallowed or had been eaten earlier.

The type of habitat has a marked influence on the nature of the food captured by juveniles up to 3-4 yr old, since the fish and cephalopod component was lower in juveniles (88 per cent.) than in adults (98 per cent.). The juveniles supplemented their diet with annelids, other molluscs, and crustaceans.

In the Port Sorell (Tas.) estuary, crustaceans (crabs) formed the major part of the stomach contents, though for a short period of each year when whitebait (*Lovettia seali* Johnson) were running the sharks also fed on these small anadromous fish.

The diet of the small sharks in the Pittwater (Tas.) estuary was more diversified and included sandworms, crabs, shrimps, small fish, and cephalopods. On two occasions the stomach contents yielded a freshly eaten fish which is normally found only around string kelp beds (*Macrocystis pyrifera* (L.) Agardh), the nearest bed being in Frederick Henry Bay about 15 miles distant from the Pittwater tagging centre.

Examination of gut contents from sharks caught near Portarlington (Port Phillip Bay, Vic.) indicated that crabs formed the most important part of their diet.

The stomach contents from juveniles caught in George Bay (St. Helens, Tas.) showed that these sharks have a much more varied diet than those found elsewhere. No doubt this is due to the environmental conditions found in the bay, where the grass wrack (*Zostera* sp.) grows well and provides shelter for a very varied fauna. Fish and cephalopods formed the bulk of the juveniles' food but snapping shrimps (*Crangon* spp.), sandworms, and the foot of the gastropod (*Scaphella undulata* Lamarck) were often found in the gut. The most commonly found food fish of the juvenile sharks were the anchovy (*Engraulis australis* Shaw), followed by the small cod (*Physiculus barbatus* Gunther) and a viviparous goby (*Arenogobius bifrenatus* Kner). The latter fish constituted a new fish record for Tasmania, yet during this investigation it was often found in the stomach contents of the juvenile sharks. Another species, *Ophiclinus gracilis* Waite, a blenny, was also a new record for Tasmania. Other species including flounder (*Rhombosolea tapirina* Gunther) occurred occasionally. A Petersen type tag which had been fastened to a 20-cm flounder released 3 months previously was found in the gut of a shark from George Bay. Not uncommonly pieces of *Zostera* sp. were found in the stomach; this was regarded as accidental.

From the beginning of this work the marked preference of sharks for very fresh bait or squid was most striking. Shark fishermen are all aware of the importance of fresh bait for baiting their long lines. Even the long storage of bait under ideal refrigeration reduces its effectiveness.

(*c*) *Internal Parasites*

One of the most noticeable and surprising features of the examination of the body cavity and gut contents of 600 school sharks was the almost total absence of helminth parasites. Only once was a body cavity parasite found; it was a larval tetrarhynchid cestode. Early in this investigation this absence of internal parasites was noticed and a thorough search was always made for them. Occasionally dead nematodes were found in the gut but these were referable to fish eaten by the sharks.

(*d*) *Total Length to Total Weight Relationship*

The mathematical relationship between length and weight of fish has been studied extensively (Hecht 1913; Crozier and Hecht 1914; Clark 1928; Hile 1936; Martin 1949).

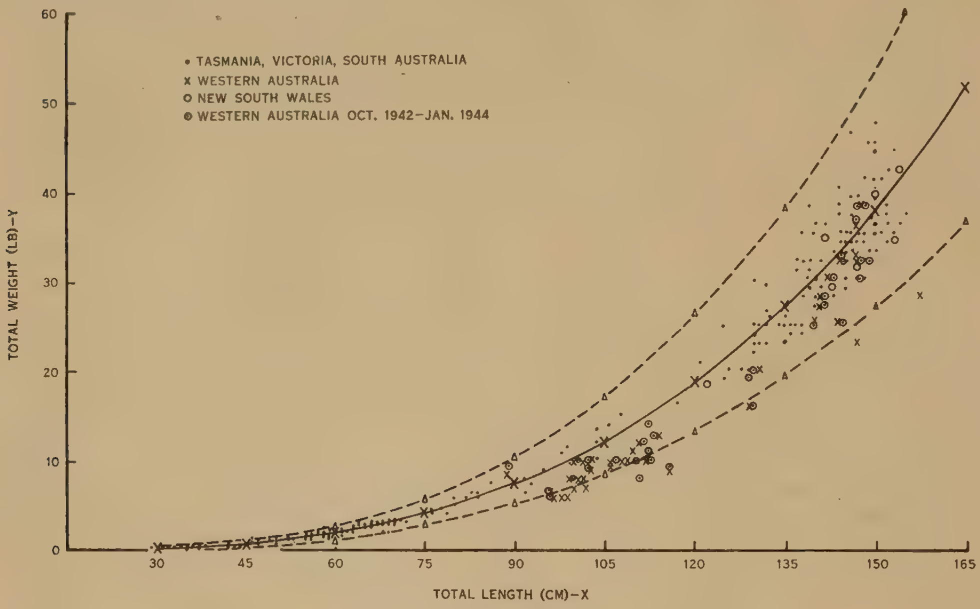

Fig. 2.—Male total length and total weight.

For most fishes it has been found that the weight increases more rapidly than the cube of the length (Keys 1928). This is also true for sharks.

The data used for computing the curves for each sex have been collected over the past 5 yr from all localities at all times of the year from sharks of all sizes in various stages of sexual maturity, so that the results are as representative as possible. As this species is ovoviviparous, measurements from pregnant females have been excluded. The total weights (y) of 278 males and 254 females at different total lengths (x) are shown graphically in Figures 2 and 3. The points plotted lie along a curve having the equation $y = ax^b$ where a and b are constants.

The equation giving the curve best fitting the data for the length/weight relationship was calculated by the least squares method. There is no appreciable difference between the shape of the resultant curves, the exponents being almost identical and the constants a very similar. The fitted curves for the data are:

Males:

$$\log y = 0.827 + 3.169(\log x - 1.940),$$

or

$$y = 4.80 \times 10^{-6}x^{3.17}.$$

Females:

$$\log y = 0.804 + 3.178(\log x - 1.925),$$

or

$$y = 4.86 \times 10^{-6}x^{3.18}.$$

The calculated weight for each specific length is given, together with the 1 per cent. fiducial limits for the weights of sharks at that length,

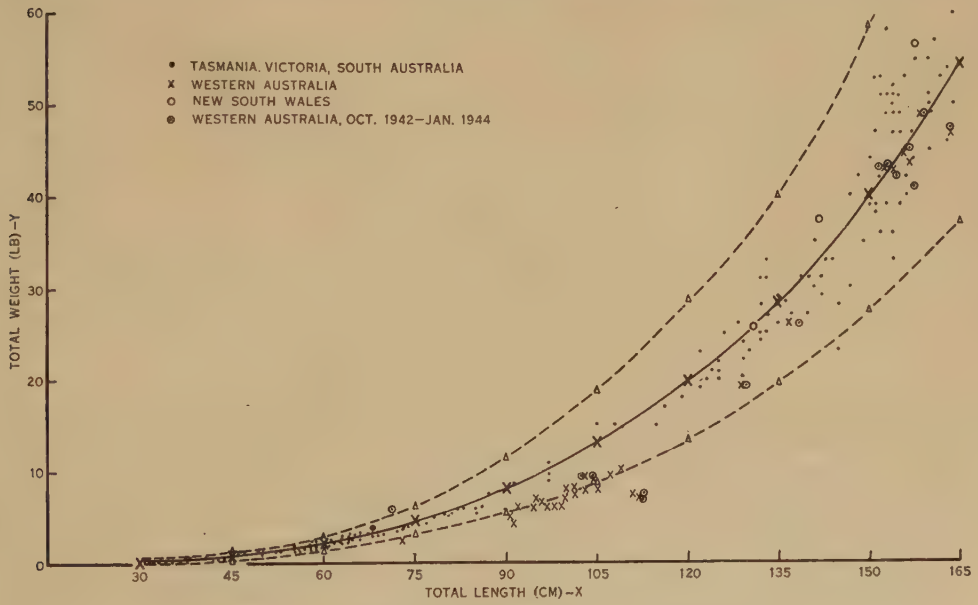

Fig. 3.—Female total length and total weight.

i.e. the limits such that the probability that a shark with that given length will lie within them is 99 per cent., this probability being based on the sample analysed. On the above figures these upper and lower limits of the variance are shown by broken lines above and below the fitted curve (mean variance) for the data collected for each sex.

Also included in the figures are plots of weights of some New South Wales school sharks caught by commercial fishing vessels during 1942-44 and those from sharks caught during 1947-50 in Western Australian waters by the research vessel *Warreen*. These biometric data have not been included in the calculations for fitting the curves to observed data.

It is interesting to note that weight increases by approximately the power 3.2 of the length in both sexes. Ripley (1946) found that the males of the American soupfin shark (*G. zyopterus*), a larger species of the same genus, increased by the same power (3.2) but there was a marked change in rate for females after sexual maturity. He stated that immature females (40-149 cm) increased in weight as the power 3.3 of the length, which was similar to the rate for the males; mature females over 150 cm increased in weight by the power 4.2 of the length. In the present study the length/weight data for each sex were treated as belonging to a uniform curve rather than to two separate curves. Ripley (1946) apparently assumed a sharp change in the weight increase per unit length

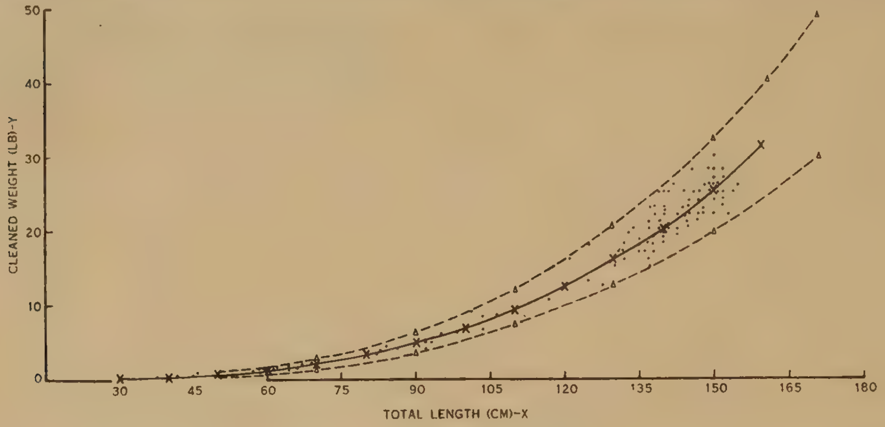

Fig. 4.—Male total length and cleaned weight.

at the onset of sexual maturity. It has been generally recognized that growth rate curves of fish show a progressive decrease with age in the slope of the curve rather than an abrupt change in the direction of the slope at maturity. It was found that there was no sharp inflexion at maturity in the shape of the growth rate curve (Fig. 19) for school sharks.

Tagging has shown that the New South Wales sharks are a part of the south-eastern Australian stock, but there is no evidence that this stock includes Western Australian sharks. From the above figures it can be seen that Western Australian sharks with lengths below 150 cm are lighter in weight than those of comparable size in the main south-eastern stock. Above this size their total weights were near the means of the weight limits. The numbers of Western Australian sharks caught have been too low to allow a separate computation of the length/weight equation to be made for comparison with that for the main south-eastern stock.

For lengths above 100 cm the divergence between the weights of the two sexes of sharks from the eastern States becomes more apparent, the females being heavier than the males. Moreover females grow larger than males since the male of greatest length measured only 155 cm and weighed 37 lb, whereas the biggest female dissected measured 164 cm and weighed 60 lb. The heaviest male (150 cm) weighed 47 lb. The longest female caught during this investigation measured 170 cm and in 2 yr commercial fishermen from Port Franklin (Vic.), caught five measuring 174 cm.

The females of the school shark grow to a greater size and weigh more than the males; and similar observations have been made about females of other elasmobranch species by Quigley (1928) for *Squalus suckleyi* Girard, by Ford (1921), Hickling (1930), and Templeman (1944) for *Squalus acanthias* Linnaeus, and by Ripley (1946) for *Galeorhinus zyopterus.*

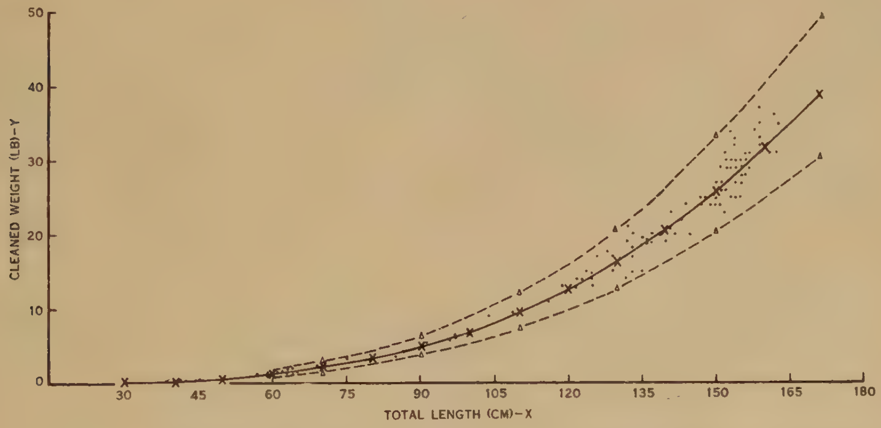

Fig. 5.—Female total length and cleaned weight.

(*e*) *Total Length to Cleaned Weight Relationship*

Power curves ($y = ax^b$) have been fitted to the data plotted in Figures 4 and 5. There is a close similarity between these two curves, which show similar trends to those in the previous figures. Differences between the cleaned weights of the two sexes are very small (0.5 lb at 135 cm). In this instance the dressed carcase of commerce, which does not contain the head, was taken to represent the cleaned weight. The power curves which give the best fit to these plotted data are:

Males:

$$\log y = 1.071 + 3.204(\log x - 2.072),$$

or

$$y = 2.71 \times 10^{-6}x^{3.20}.$$

Females:

$$\log y = 1.059 + 3.233(\log x - 2.066),$$

or

$$y = 2.39 \times 10^{-6}x^{3.23}.$$

The broken lines indicate 1 per cent. fiducial limits.

(*f*) *Total Weight to Cleaned Weight Relationship*

In both sexes the cleaned weight had a constant and almost linear relation to the total weight. Few sharks of the range 10-20 lb (90-120 cm) were taken (Figs. 6 and 7); but as the remaining data fall along a line which varies only slightly from linearity it may be safely concluded that the interpolation over this range is valid. As expected the exponents are close to 1 and the curves very nearly straight lines, viz:

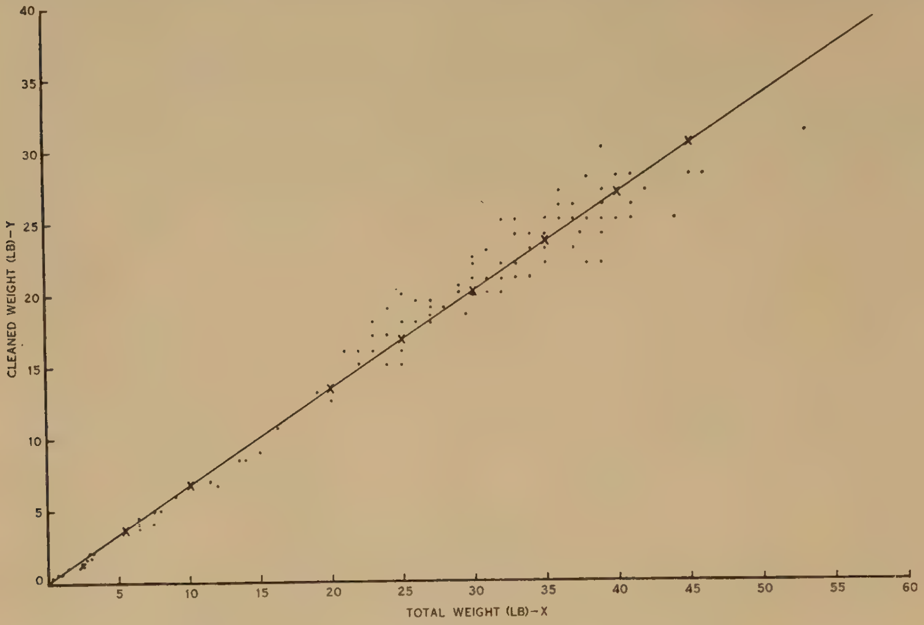

Fig. 6.—Male total weight and cleaned weight.

Males:

$$\log y = 1.082 + 1.014(\log x - 1.259),$$

or

$$y = 0.639x^{1.01}.$$

Females:

$$\log y = 1.061 + 1.012(\log x - 1.256),$$

or

$$y = 0.617x^{1.01}.$$

In the female there is a slightly greater amount of so-called "commercially useless" flesh than in the male. According to the formulae 64.5 per cent. of the male carcase is marketable as against 62.3 per cent. in the female. These values for the marketable proportion of the flesh do not include the liver weight, which for the above relationship was considered as a part of the discarded viscera, although the liver has a definite commercial value.

Not all of the cleaned weight of a shark is edible since the vertebral column, fins, and skin have still to be removed. Filleting losses are 30 per cent. of the cleaned weight so that only about half the total weight of shark (approximately 45 per cent.) is available for food. The loss due to filleting was determined from a buyer's records over a period of 2 yr.

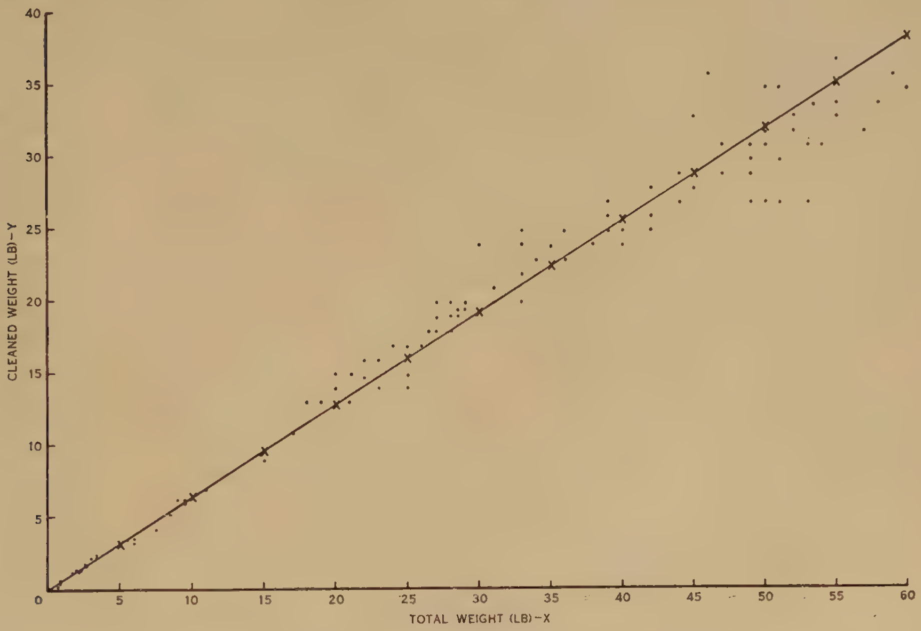

Fig. 7.—Female total weight and cleaned weight.

In some crayfishing areas the heads of school sharks are often sold for bait. At these ports the economic return for the shark carcase is higher than elsewhere, for the mean weight of the head of an adult school shark (to first gill slit) is 7 lb.

(*g*) *Cleaned Weight to Liver Weight Relationship*

Marked sexual differences are apparent in the liver weight of sharks for the same cleaned weight; the female liver is heavier than the male and remains so throughout life. The curves for the above relationship for both sexes are given in Figures 8 and 9.

The regression equation of the form $y/x = a + b(x - \bar{x})$, where x = cleaned weight (lb) and y = liver weight (oz), was used because with y/x the variance was stabilized. Both curves gave a good fit to the observed data and the within variances, tested by Bartlett's test, were homogeneous. The formulae for the derived curves were:

Males:

$$y = 0.0476x^2 + 1.07x,$$

Females:

$$y = 0.0763x^2 + 1.02x.$$

By using the formulae and deriving the mean liver weight for various cleaned weights it is possible to express the liver weight as a percentage of the cleaned weight. Table 1 shows that in fully grown non-pregnant females (32 lb) the liver represents one-fifth of the cleaned weight of the shark. The heaviest male liver obtained weighed only 80 oz whereas the heaviest female liver was 196 oz (12¼ lb). The fluctuation in weight was considerably less in the male than in the female, which was influenced markedly by sexual development and the stage of pregnancy.

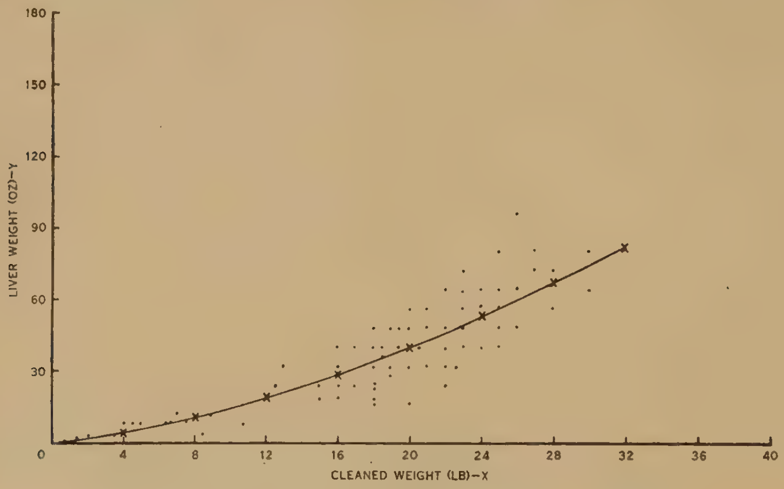

Fig. 8.—Male cleaned weight and liver weight.

There was a significant difference between liver weight to cleaned weight ratios of pregnant females with full-term embryos and non-gravid females. In a sample of 11 gravid females from the one locality in the same month, with cleaned weights of 26-37 lb, there was a range of 5.7-11.1 per cent., mean 8.1 per cent., in liver to cleaned weight ratios; whereas for non-gravid females with the same cleaned weights the ratio showed a range from 14.6 to 24 per cent. (calculated).

TABLE 1
LIVER WEIGHT AS PERCENTAGE OF CLEANED WEIGHT (CALCULATED)

Cleaned Weight (lb)	Liver Weight	
	Males	Females
4	7.7	8.2
8	8.8	10.1
16	11.4	14.0
32	16.2	21.6
36	—	23.5

In general the female liver was largest prior to ovulation and decreased in size during the gestation period to a minimum size and weight (½-1 lb) immediately before the birth of its young. For that reason the liver size was one of the criteria used to assess the probability of recent parturition in females caught during November and December.

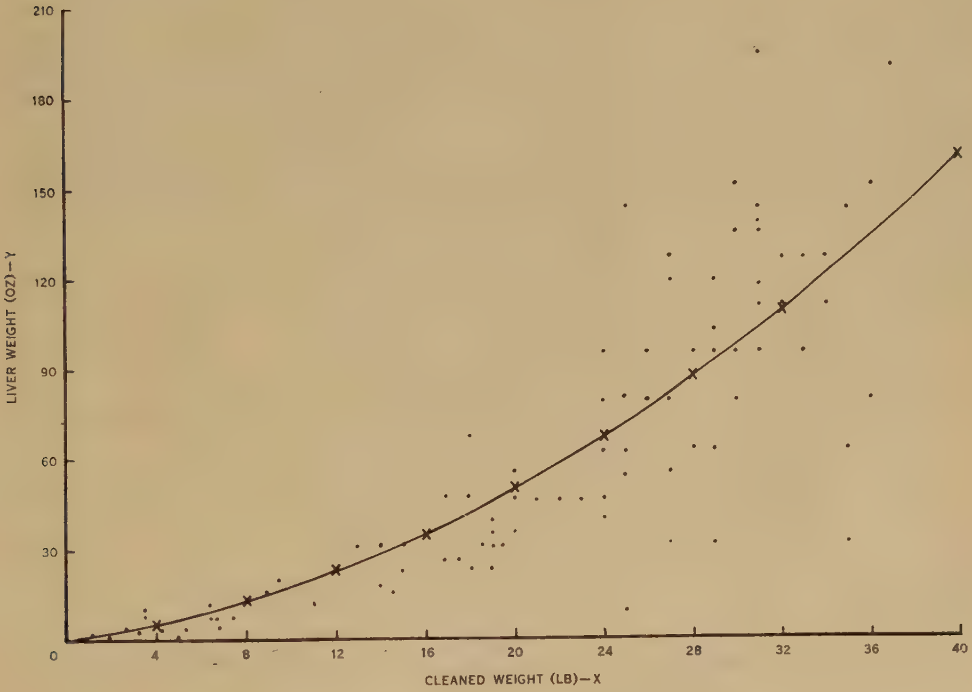

Fig. 9.—Female cleaned weight and liver weight.

(*h*) *Length at Sexual Maturity*

Males.—In the male the transition from adolescence to maturity took place over a fairly extensive size range. The smallest male with "running milt" measured 121 cm though larger ones were often found to be immature. All males over 132 cm were mature.

Macroscopically, the maturity stages are easily determined during the late summer and early autumn months when the testes are enlarged and the seminal vesicles contain active spermatozoa. In the early summer months the seminal fluid flows freely from the cut surface of the testis. The determination of sexual maturity in sharks which were maturing or had just matured was often difficult at other seasons. In some of these doubtful cases stained sections of portion of the testes were used to determine sexual maturity. By this method it was possible to see when spermatozoa had matured because all stages of spermatogenesis were present. Mature tissue differed from the immature by the presence of enlarged seminiferous tubules which carried bundles of ripe spermatozoa from their inside walls or had them free in the lumen of the tube. The spermatozoa were attached by their head ends and their tails extended freely into the centre of the tubules. Specimens showing this stage of development were considered to be sexually mature. None below 120 cm was found and hence it was considered that this length represented first maturity in the male.

As the numbers of sexually mature specimens determined by histological methods were small compared with the number dissected no attempt was made to estimate the percentage maturity at a given length over the size range 120-132 cm. The results were confined to the determination of length at first maturity. As the maximum length of males examined was 155 cm, they are three-quarters grown before sexual maturity is reached.

Females.—The criteria used for determining sexual maturity in the female were:

(i) The presence of embryos in the uteri;
(ii) The presence of larger eggs containing yellowish yolk among the uniform pale grey eggs ("sago grains") within the reproductive tissue of the single ovary;
(iii) The developmental stage of the two uteri, shell glands, and size of the opening of the median funnel of the oviducts.

As in the male there were stages where the maturity was easily defined but where it was doubtful an examination of all the reproductive organs was necessary to determine the sexual state. Using the above criteria no female less than 135 cm was found to be sexually mature. An occasional female between 135 and 138 cm exhibited one but not two of the above conditions of maturity and was therefore of doubtful maturity.

(*i*) *Size of Ovarian Eggs and Onset of Sexual Maturity*

Usually mature school sharks of different lengths from the same catch had similar-sized large ovarian eggs. However, other catches made elsewhere about the same time included mature sharks whose ova differed quite markedly in size and colour. For instance in June 1949, long line sets were made at three localities within a range of 150 miles. The second and third sets were made 2 and 6 days respectively after the first and the variation in measurements of the ova diameter from these sharks have been summarized in Table 2.

The condition of the ovaries of those females caught in set No. 2 indicated that these large ova (40-50 mm dia.) were almost ready for ovulation whereas the ovaries from the other females were not. In fact the ova diameter sizes of the latter females were comparable with those found in the ovaries of females carrying full-term embryos. Measurements of ova diameter from seven females ranging in size from 144 to

163 cm caught at Pittwater in December 1951, just before or shortly after release of their pups, showed a size range of 10-14 mm. Measurements of ova sizes made in gravid females from other areas showed a similar range in diameter. This small size of ova was interpreted as showing that those females would not ovulate that breeding season.

It was found that all sizes of unextruded ova up to 40 mm in diameter may be encountered at any period of the year though the larger sizes were more frequently observed during the late summer and autumn months of the year (Table 5). Large ova observed at times other than these months showed a much more intimate connection with the ovarian tissue than ova ready for extrusion, which were very loosely held by the reproductive tissue. The former condition may possibly indicate a delay in the time of ovulation and as a consequence the ova diameter measurements were of limited value in determining time of ovulation. Their value in this work was that they indicated the onset of sexual maturity because the yolk content increased their size and coloured them yellow; the immature sharks had no yellow ova whatever.

TABLE 2

DIFFERENCE IN SIZES OF OVA FROM FEMALES CAUGHT WITHIN 5 DAYS AT DIFFERENT LOCALITIES

Set No.	Sample No.	Size Range (cm)	Range of Diameter of Largest Ova (mm)
1	4	151-160	12-18
2	13	147-162	40-50
3	8	145-163	10-20

Although measurements of the length and width of the ovarian reproductive tissue were useful indicators of the change from adolescence to sexual maturity, they were unsatisfactory as criteria for the precise determination of sexual maturity at a specific length, for the size of ovarian tissue was dependent upon the number and size of the developing ova.

Therefore in determining the length of the smallest female to reach maturity, the more important criteria were: (i) ova diameter, and (ii) the degree of attachment of large ova. It is considered that some females reach first maturity at 135 cm although the majority are still immature at this length. The smallest gravid female encountered throughout this investigation was 144.5 cm.

The difference in lengths at first maturity of males and females (15 cm) was the same as that reported by Ripley (1946) for *G. zyopterus*. In the latter species the smallest mature males were 135 cm and the females 150 cm.

Between the two species, *G. australis* and *G. zyopterus*, there was a remarkably close similarity in the ratios of length at first maturity to maximum length in each sex. This led to a comparison of ratios between two species of the genus *Squalus* Linnaeus, the data used being extracted from published work on these species (Table 3).

From Table 3 it can be seen that within these two genera the ratios of length at first maturity to maximum length for both sexes are extremely close and could be constant for each genus. Because of the paucity of data on elasmobranch species it is not possible to check this ratio for other species of the same genus.

TABLE 3

RATIOS OF FIRST MATURITY FOR TWO GENERA OF ELASMOBRANCHS

Species	Males			Females			Source of Data
	Length at First Maturity (cm)	Maximum Recorded Length (cm)	Ratio	Length at First Maturity (cm)	Maximum Recorded Length (cm)	Ratio	
Galeorhinus australis	120	155	0.77	135	174	0.775	
Galeorhinus zyopterus	135	185	0.73	150	195	0.769	Ripley 1946
Squalus acanthias	59	83	0.71	71	110	0.645	Ford 1921
Squalus suckleyi	72	100	0.72	78.5	130	0.604	Sato 1935
					124	0.633	Bonham *et al.* 1949

Should confirmation be forthcoming that other elasmobranch species exhibit similar ratios, a useful application of the principle can be made. So long as the ratios are known for one species and the maximum lengths of the two sexes of the second species are known it is possible to derive mathematically a theoretical value for the onset of sexual maturity in the two sexes and thereby save much laborious field and laboratory work. The saving in time thus effected could be spent on more exacting examinations of specimens of which the lengths are close to the calculated value at first maturity.

It is obvious from Table 3 that the males reach sexual maturity at a length about three-quarters of their known maximum length whereas in the female the onset of maturity is a characteristic of the genus to which it belongs. This ratio apparently varies from two-thirds to three-quarters of the maximum length of the species in a genus.

(*j*) *Time of Ovulation and Fertilization*

It has been shown by Ford (1921), Hickling (1930), and Templeman (1944) that there is a positive correlation between size of the ovarian egg and time of ovulation in the spiny dogfish, *Squalus acanthias.* They found that there is a definite period during which ova are maximum in size and the embryos are fully developed. From their work they infer that fertilization of the eggs takes place almost immediately after the birth of the young. On the other hand, ova of the school shark are smallest (10-16 mm) at the time of parturition which, in Victorian and Tasmanian waters, is during the late spring months. Measurements of ova from 17 females carrying full-term young caught in December near Flinders I. (Bass Strait) and Pittwater (Tas.) showed a very limited diameter range (9-16 mm, mean 11 mm, Table 4). The ova of non-pregnant females were larger, the diameter range being 20-40 mm (mean 34 mm, Table 5).

TABLE 4

OVA DIAMETER OF FEMALE SCHOOL SHARKS CARRYING FULL-TERM YOUNG

Date	Flinders I.			Pittwater		
	No. Examined	Diameter Range (mm)	Mean (mm)	No. Examined	Diameter Range (mm)	Mean (mm)
Dec. 1948	4	9-16	11			
„ 1949	1	10	10	2	10-15	12
„ 1950				3	10-14	11
„ 1951				6	9-15	12
„ 1952				1	10	10
Total	5	9-16	10	12	9-15	12

No female carrying full-term young had normal ova greater than 16 mm in diameter; in one abnormal female ovarian eggs 35 mm in diameter were found but they were undergoing resorption.

The ova sizes of the school shark could not be used in a similar manner to those of *Squalus acanthias* to indicate the time of ovulation. However, a study of the male sexual cycle assisted with the determination of the possible time of copulation and subsequent fertilization.

From late July till about December the testes of mature males are slowly filling, and by about March and April in Victorian and Tasmanian waters (south-eastern Australian area) reach their maximum size (comparable stages are 2-3 months earlier in South Australian waters (Table 5)). During the following May and June the seminal vesicles become distended with spermatic fluid, which is readily discharged when these sharks are landed on the decks of fishing vessels.

It can be seen in Table 5 that the period when males are "running ripe" is approximately of 3 months' duration. Practically all males in all waters have discharged seminal vesicles ("spent") by the end of July.

TABLE 5

RIPENESS OF MALE GONADS AND OVA DIAMETERS OF SCHOOL SHARKS

Month	No. of Males Expelling Milt When Landed				Maximum Diameter of Ova			
	SE. Australia		Sth. Australia		SE. Australia		Sth. Australia	
	No. Examined	No. "Running" Ripe	No. Examined	No. "Running" Ripe	No. Examined	Range in Dia. of Ova (mm)	No. Examined	Range in Dia. of Ova (mm)
Jan.	85	—			22	9-30		
Feb.	36	—			8	3-45		
Mar.	52	—	56	4	4	7-13	10	12-45
Apr.	45	—	160	41	2	10-12	63	2-29
May	118	24			9	13-50		
June	97	38			33	4-50		
July	22	4			2	13		
Aug.	12	—			1	20		
Sept.	22	—			1	9		
Oct.	28	—			7	12-30		
Nov.	4	—			2	17-30		
Dec.	71	—			10	20-40		
Total	592	66	216	45	101		73	

The onset of "ripeness" in the male is earlier in the warmer waters of South Australia than in the colder waters of the south-eastern Australian area. Likewise ovulation is earlier in South Australian waters, because recently ovulated eggs and small embryos up to 12 cm in length were encountered during the latter part of March whereas comparable stages in the main area are not found until July and August. Since the investigation was carried out in the main centre of the fishery any deductions about gonadal development made from these results are also applicable to South Australia, though the stages occur earlier there than elsewhere.

In the waters of south-eastern Australia, where most mature males have discharged seminal vesicles in July, it follows that copulation and subsequently fertilization must occur only a short time beforehand when the distended seminal vesicles readily discharge their spermatic fluid and the claspers are turgid and bloodshot. From this condition it is deduced that the copulatory act occurs some time during May or June. During this period good hauls from long line sets near the edge of the continental shelf are made by fishermen but subsequently the catches fall off with the dispersal of the sharks. This behaviour of aggregating is analogous to the shoaling behaviour of many teleostean fish, with dispersal after they have spawned.

Strong circumstantial evidence in support of copulation taking place during these 2 months in Victorian and Tasmanian waters was obtained in June 1949 from a 150-cm female with ovarian eggs 45 mm in diameter (Table 2, set No. 2). The necks of the two uteri and the cloaca contained a foreign fluid which was identical macroscopically with the seminal fluid of the males caught during the same set. Unfortunately there were no facilities aboard for examining the fluid microscopically.

Considering all the available facts it is evident that the mature females ovulate and fertilization takes place during May and June in the colder waters of the two southern States.

(*k*) *Parturition*

From July to December, embryos in various stages of development may be found, the very early stages being taken less frequently than the more advanced and full-term embryos. This is particularly so in the more southern waters around Tasmania, though in South Australian waters the younger stages are more easily obtained and the reason for their greater availability is explained in a later section as being due to their migratory behaviour.

The actual period of parturition or "pupping" varies from year to year, December being the main month in Tasmanian waters. Table 6 shows the results of the examination of 64 females caught in various pupping localities around the Tasmanian coast during the period 1946-52.

Included in Table 6 were some females who had already given birth to their young. However, they all showed unmistakable evidence, such as the presence of the empty thin-walled egg capsule in the enlarged uterus with its complicated plexus of blood vessels, that they had "pupped" only a short time before. The five females caught in September and October had embryos still exhibiting the external yolk sac which indicated that these young had not reached full development. Full-term young have no external yolk sac. The females were recorded in the table under the month they were caught as there is no evidence on the time taken for the absorption of the small yolk sac and the subsequent birth of the young.

TABLE 6

TIME OF PARTURITION IN TASMANIAN WATERS

Month	No. of Females caught in Nursery Areas
September	1
October	4
November	10
December	47
January	2
February	—
Total	64

A disturbing fact emerged from the study of ova size, period of gestation, and parturition: it became apparent that not all mature females carried young each year. This was checked by fishing near known "nursery areas" during November and December, when both gravid and non-gravid females were caught together. The non-gravid females carried ovarian eggs in all sizes up to 40 mm, and the manner in which the largest eggs were embedded in the tissue of the ovary indicated that they were not yet ready for ovulation. It was believed that these large eggs remained in a relatively dormant condition until the following May or June.

The ratio of gravid to non-gravid females varied from area to area. An analysis of all adult female sharks dissected showed that only about half of them carried young during the period July to December, so that it must be concluded that the school shark has a low reproductive capacity.

(*l*) *Fecundity*

The three ways in which the reproductive capacity of mature female sharks can be assessed are: (i) ovarian egg counts, (ii) embryo counts, and (iii) full-term "pup" counts.

The full-term "pup" count was used in this investigation, as the ovarian egg count was considered to be subject to too many errors and there was a scarcity of material for (ii). Even with full-term embryo counts errors due to premature births before the females were hauled inboard could occur, but by rigidly excluding from the counts any females suspected of premature birth this error was reduced to a minimum. All such counts were made on sharks caught during experimental fishing operations, and hence maximum control was exercised over the fishing time and the method of handling the gravid females caught.

In practice it was found that a strong twine tied tightly round the body at the cloacal opening compressed together the pelvic fins and by constricting the opening of the cloaca prevented the premature birth of the full-term embryos. Because of this rigid exclusion of suspect material the data presented below were necessarily limited, namely, 33 adults and 942 full-term "pups".

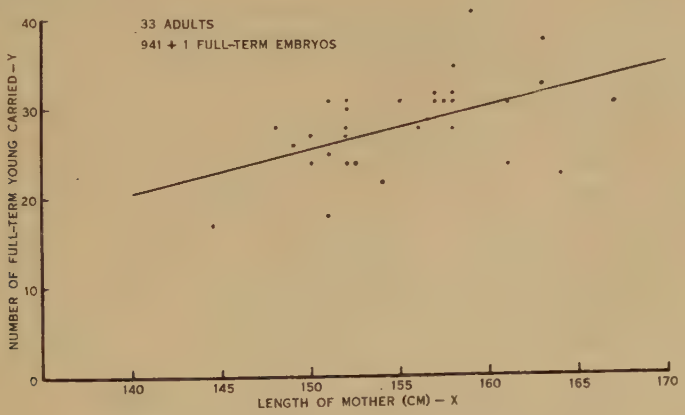

Fig. 10.—Fecundity of the female school shark.

In Figure 10 the length of the mother (cm) was plotted along the abscissa and the total number of living young each parent carried on the ordinate. Each point represented the number of living young carried by each mother of a specific length.

From an examination of Figure 10 it can be seen that a straight line fits these plotted data. The linear regression line calculated by the least squares method and fitted to these points is: $y = -50.0 + 0.505x$. From this formula it is deduced that for each 2-cm increase in length the number of pups carried increases by one. The mean length of the mother and mean number carried for the sample analysed is $\bar{x} = 155$ cm and $\bar{y} = 28.4$ young.

Statistically the linear hypothesis adequately represents the data, and the value of the slope 0.505 is significantly different from zero (probability is less than 1 per cent.). The 5 per cent. fiducial limits for the slope are 0.201 and 0.809, i.e. in 95 per cent. of mature sharks the number of young increases by one for an increase in length of between 1.2 and 5 cm in the mother.

The 33 gravid females were caught in widely separated areas over 5 yr. Twenty-five were long-lined in Pittwater, near Hobart, while they were coming into a deep channel to give birth to their pups. The highest number of young carried was 41, taken from a female 159 cm long, whilst the lowest was 17, taken from the smallest recorded gravid female, 144.5 cm long.

Ripley (1946) reported that most undeveloped eggs occurred in the posterior part of the uteri of *G. zyopterus,* whereas in *G. australis* over three-quarters of the undeveloped eggs or embryos, dead from arrested development, were in the anterior third of the uteri. The presence of these dead embryos did not seem to affect the development of the living ones close to them. Similar observations about this lack of effect on living embryos in the uteri were made by Templeman (1944) on the spurdog, *Squalus acanthias.* It was interesting to note that almost twice the number of undeveloped eggs or dead embryos occurred in the right uterus. No smell of putrefaction or decay was noticeable in any of these abnormalities.

Two sharks were found with only one functional uterus, one the right and in the other the left. Both were caught at Pittwater, one in 1949 and the other in 1951. The appearance of the mass in the non-functional uterus resembled a tumorous growth but on closer examination and dissection it was possible to remove pieces of translucent membranous material which closely resembled the structure and appearance of the shell membrane or envelope of the normal embryo. The dark yellow-brown structureless mass felt greasy to the touch. It was considered to be yolk undergoing changes. Histological sections prepared from the mass in the uterus of the first shark were examined by a pathologist, who reported that the appearance was unlike any recognizable tissue structure. It was not until the second specimen was secured that the mass was identified as altered yolk from undeveloped eggs in which was mixed pieces of the envelope secreted by the shell gland. These were extreme examples of non-development of the eggs.

(*m*) *Size of Embryos in Relation to Total Length of Mother*

In Figure 11 the mean length of the full-term embryos from each mother (y) has been plotted against the mother's total length (x).

Because of the necessity to exclude all doubtful instances of premature birth, the data so used are not comprehensive enough to permit a mathematical analysis of this relationship. While it is inconclusive, there is some evidence to suggest that the larger mothers have larger pups.

Excluding two obvious instances of arrested development the maximum size range of full-term embryos from any one parent was 50 mm. However, the majority of embryos from any one mother showed a more limited size range, of only 30 mm.

(*n*) *Effect of Position in Uterus on Length of Embryo*

There was no difference between the mean lengths of full-term embryos from the left and right uteri in each parent. Although Ripley (1946) found differences of the order of 53-79 mm in the right uterus and 52-75 mm in the left uterus in the lengths of one-quarter grown embryos of *G. zyopterus,* no such comparable differences were found in three-quarter to full-grown embryos of *G. australis.*

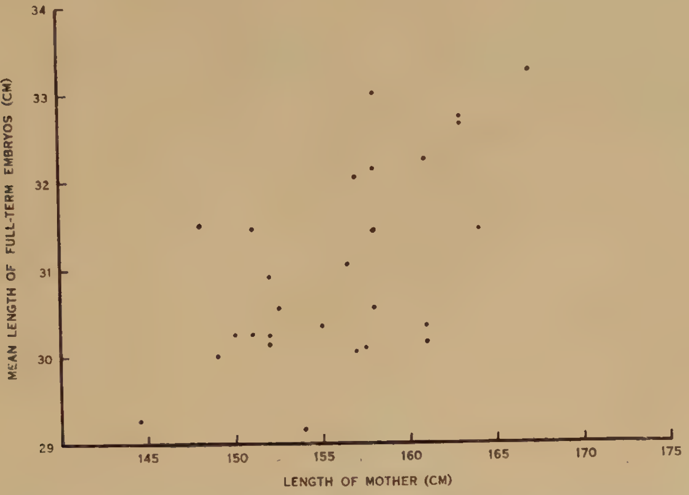

Fig. 11.—Size of full-term embryos in relation to total length of mother.

A simple linear regression analysis of length of the embryo on its position in the uterus was carried out on each of the 52 samples. Individually only seven of these regression coefficients were significant but all were negative. A statistical test applied to the data showed them to be homogeneous, and the 52 samples could legitimately be supposed to be a random sample. Analyses showed that the length of every fourth embryo decreased by approximately 1 mm from the posterior end of the uterus forwards. There is therefore a correlation, albeit small, between the position of the embryo in the uterus and its total length.

(*o*) *Length Frequency of Full-term Embryos*

In preparing the male and female length frequency curves in Figure 12 941 full-term embryos taken from 33 mothers were used. One embryo of unknown sex was omitted from the sample used in Section IV(*k*).

The curves of the 491 male and 450 female length frequencies were very similar, indicating that, at birth, there was no size difference between male and female "pups". No significant size difference had been detected between the two sexes within each parent. Ford (1921) and Templeman

(1944) were both unable to find any difference in the sizes of the two sexes in *Squalus acanthias,* which were born in equal numbers. The same was true for *Squalus suckleyi* (Bonham *et al.* 1949).

The modal length of these two curves is 300 mm, the frequency range extending from 260 to 350 mm. However, two females (260 and 270 mm) and one male (270 mm) showed unmistakable signs of arrested development (larger yolk sac and smaller size). If these are excluded from the sample studied, the size range of normal embryos is between 280 and 350 mm.

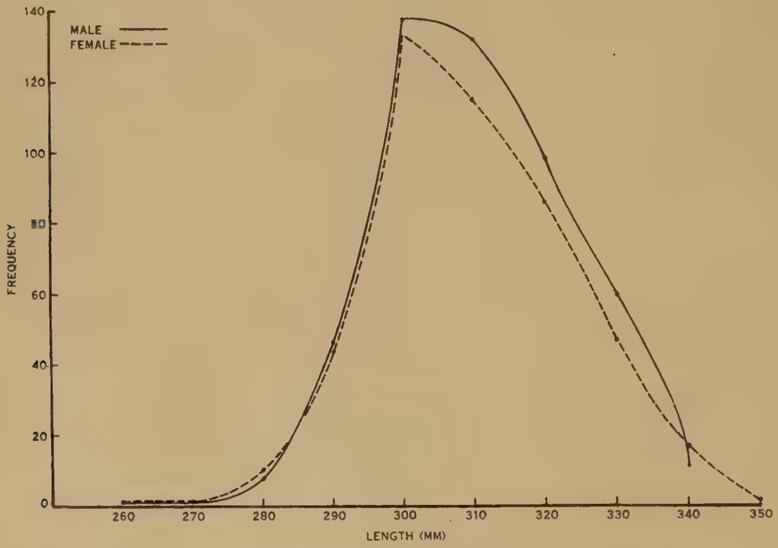

Fig. 12.—Length frequency curves of male and female full-term embryos.

The measurements on the 941 embryos were obtained over the past 5 yr, and a comparison of the length frequencies obtained in each of the years 1948-51 inclusive showed that, with the exception of 1949, when the mode was 310 mm, all curves exhibited the same characteristics as Figure 12. In all accounts there were more male than female embryos.

Since there was no length difference between the two sexes in the full-term embryos it may be deduced that during their intra-uterine development growth rates of the males and females are similar.

Although the curves appear asymmetrical the data when subjected to statistical analysis indicate no reason to believe the samples other than normal.

(*p*) *Length Frequency of Recently Born Pups*

The sizes of recently born males and females of the school shark caught on handlines in the nursery areas show the same type of length frequency curve as those for full-term embryos (Fig. 12). As expected, the changed position of the mode has indicated an increase in size and values varied according to time of pupping in each year. These free-living pups caught shortly after birth showed the same characteristics as the full-term embryos with regard to the proportions of the different sexes.

TABLE 7

SIZES OF JUVENILE SHARKS CAUGHT BY DIFFERENT GEARS

Length (cm)	Mesh Nets (2¾-4½ in. mesh)				Handlines (No. 4 "Mustad" hooks)			
	No. Tagged		No. Recaptured		No. Tagged		No. Recaptured	
	♂	♀	♂	♀	♂	♀	♂	♀
30								
31								
32								
33						1		
34					4	4		
35		1			7	4		
36	1	1			4	7		
37	1				7	4		
38	1	6	1		3	4		
39	5	5			4	4		
40	8	5	1			4		
41	4	3			1			
42		6		1	1	1		
43	2	2	1	1				
44	2	4						
45	2	3						
46	3	4		2		1		
47	2	5		1	1			
48		7		2	1	1		1
49	2	5	1	1				
50	8	5	3			5		1
51	5	4	1	1		7		1
52	12	5	3	3	5	1	1	
53	1	3	1	2	7	4		
54	3	5		1	4	8		
55	6	12	5	2	10	9		1
56	8	12	1	4	9	12	2	2
57	7	7	1	2	16	15	2	1
58	13	11	4	4	11	11	2	1
59	9	6	2		12	14		1
60	4	5	2	2	14	10	1	2
Total	109	132	27	29	121	131	8	11

The males were in excess of the females (54: 46). However, the longer the period between their birth and subsequent capture the closer to parity became the number of males and females caught. After a year there were more females than males caught. This could indicate that the death rate was greater among males than females, or alternatively, that the gear used in the different areas was more selective for females. However, this latter assumption is considered unlikely because such a wide range of sizes has been caught by both handline and mesh net gears (Table 7) and because observations in all areas have not shown any difference in behaviour of the male and female juveniles or in their body proportions.

Between the first and second year after birth, the ratio of females to males was 54:46, a reversal of the ratio immediately before birth. It is believed that these results are independent of fishing gear, which appeared to be non-selective for size and sex of the juveniles during their inshore phase. The sampling had been carried on over 4 yr in the estuaries of Pittwater, Port Sorell, George Bay, and Portarlington. Because of insufficient material for comparison the ratio of females to males in the larger size-groups which had left their sheltered inshore nursery areas was not determined.

It was noticed, however, that the time of pupping in any year tended to be later in the more southerly latitudes. Between areas in New South Wales and South Australia and southern Tasmania this difference was as much as 2 months.

(*q*) *Size Distribution*

The habit of these sharks of congregating in schools predominantly of one sex with a relatively small range of sizes is probably responsible for its common name. This schooling behaviour is always more apparent in the off-shore phase of their life cycle although the same habit tends to show up early with juveniles in the estuaries.

In Port Sorell the recently born pups (30-38 cm) were mostly located towards the upper limits of a marine-dominated environment and the larger sizes to 70 cm were found at the entrance of the estuary, which formed a part of the wide bay. The rivers flowing into this estuary are not large and even after flood conditions from heavy rains there is a quick return to marine domination.

The distribution in the other estuaries differed considerably from that found at Port Sorell. In George Bay (St. Helens) no very small juveniles were located, all those caught ranged in size from 40 to 70 cm, whereas in Pittwater all sizes from recently born juveniles through to large adolescents were present. The wide range of sizes found in Pittwater was probably due to its position, for it opens by a narrow entrance into the large and deep Frederick Henry Bay, itself a well-protected expanse of water (Admiralty Chart No. 809), and draws from it a proportion of the larger sizes frequenting this bay. Even though the larger juveniles range throughout Pittwater, the juveniles born that year mostly confine themselves to a deep, wide channel (gutter) near its entrance. At its far end the channel ends abruptly and the juveniles tend to congregate into this *cul-de-sac* to feed on the small fish retreating into this deeper water with the falling of the tide. They are easily handlined then for tagging purposes. In this channel the aggregation of young less than 1 yr old may be due, in part, to the habit of the females in giving birth to their young in a very restricted area.

In their off-shore phase the schooling habit is more pronounced and in general the sizes of the sharks in the different schools in eastern Bass Strait are found to be significantly smaller than those in western Bass Strait and South Australia (Appendix IV). The schools from the former area contain a high proportion of immature fish whereas the proportion is low in the other areas. Taken over the year, the size frequency of sharks landed at the various sharking ports along the Victorian coastline increases from east to west; likewise the assays of vitamin A potency of bulk liver samples increase the further the port is westwards along the coast (C. Kuchel, personal communication). It is known that the potency increases with size and these analyses support the evidence on the size distribution in Bass Strait. These results will be discussed in greater detail in a later publication. In southern Tasmanian waters, the sharks caught are mostly adults and therefore have a larger size frequency than those from eastern Bass Strait.

V. Migration from Tagging Operations

The tagging methods used in this investigation have been described previously (Olsen 1953). In order to follow their migration 5862 school sharks of all sizes were released. The releases may be separated into two groups, those of inshore origin (4755), which were mostly juveniles, and the off-shore releases (1089), which were predominantly adults. So far 237 tags (4 per cent.) have been returned (31.v.53).

(*a*) *Inshore Tagging*

The populations of four selected estuaries were studied intensively for 4 yr. In the three Tasmanian areas, Port Sorell, St. Helens, and Pittwater, the stocks were sampled monthly and as many fish as possible tagged and released again. During the period 1947-51 inclusive, only a week's annual visit was made to the fourth estuary, Port Phillip Bay (Vic.), when fishermen reported the presence of large numbers of juveniles. In all estuarine areas sampled the fishing gear was considered to be non-selective for size and sex (Table 7). Absolute proof of non-selectivity cannot be provided but it appears from the data to be a reasonable assumption.

Similar results from various other inshore areas sampled have confirmed those already obtained in the above four estuaries. It has been found that the movements of the juvenile school sharks followed a very similar pattern. Some differences in behaviour occurred from area to area but these are only adaptations to local environmental conditions.

TABLE 8

NUMBER OF SHARKS TAGGED AND RETURNS FOR INSHORE AREAS 1947-52

Superior numerals represent tagged sharks recovered in respective groups

Area	1947	1948	1949	1950	1951	1952	Total	Total Tag Returns (%)
Portarlington (Vic.)	618^{32}	130^{6}	241^{6}	631^{29}	456^{29}	—	2076^{102}	4.9
Pittwater (Tas.)		252^{2}	311^{3}	339^{8}	240^{6}	48	1190^{19}	1.6
Port Sorell (Tas.)		273^{3}	353^{4}	318^{3}	62^{2}	77^{2}	1083^{14}	1.3
St. Helens (Tas.)			29^{5}	154^{29}	128^{26}	15^{2}	326^{62}	19.0
Miscellaneous areas:								
Gordon (Tas.)	1				1	1	3	
Frederick Henry Bay (Tas.)		4					4	
Hobart (Tas.)		2					2	
South Arm (Tas.)				11^{1}			11^{1}	9.1
Coles Bay (Tas.)				17			17	
Stanley (Tas.)		12					12	
Hunter Is. (Tas.)			9				9	
Westernport (Vic.)	2						2	
Frankston (Vic.)			1				1	
Lakes Entrance (Vic.)		1					1	
Port Fairy (Vic.)		11					11	
East Bass Strait (Kent Group, Tas.)		4					4	
Port Davey (Tas.)			3				3	
Total	621^{32}	689^{11}	1470^{70}	887^{63}	947^{18}	141^{4}	4755^{198}	4.16

The number of sharks released at each of the various inshore areas, together with their respective tag returns, are listed in Table 8.

The 102 returns obtained from the sharks released near Portarlington in Port Phillip Bay have given the most detailed movements of juveniles in any estuary. In this extensive area of water, 31 miles long (Fig. 13), the fishing effort is fairly evenly distributed throughout and the returns obtained indicate a comprehensive sampling of the juvenile shark population.

In the summer months the sharks are always widespread but with the approach of autumn they tend to move into the channels, in one of which tagging was concentrated. Even as early as March this movement is apparent and marks the beginning of a leisurely movement of juveniles to the open sea, where they spend the winter in the deeper coastal waters.

After the release of tagged sharks in March in the Corio Bay Channel off Portarlington, returns were received earlier from all along the eastern shore than elsewhere, indicating that the main body of juveniles moved eastwards although some used alternative routes to the sea. One of these follows the more direct West channel through the numerous sandbanks to join with the South Channel near the entrance of the bay. Another route which they follow skirts the north-western shore. It crosses to the eastern shore at the head of the bay and follows it down to merge later with the main body going out to sea through the South Channel. These main routes are shown semi-diagrammatically in Figure 13.

On these routes the actual location of 84 Bay tag returns (arrowhead) are indicated with a symbol representing the year of release. In one instance the same shark was recaptured twice within 8 wk, on the first occasion off Mornington after 5 wk of freedom and on the second 17 miles to the north near Hampton 3 wk later. This movement suggests that the juveniles mill around on this eastern shore before departing for the open sea.

That the movement is seawards is shown by the greater number of June returns in the lower reaches of the Bay. Circumstantial evidence to support this theory is given by the almost complete absence of small juveniles from catches of Bay long-line fishermen during late July and August.

Their spring return to the bays follows much the same pattern as their autumn departure and the locations of such tag returns in September and October are indicated in Figure 13.

Not all small sharks return to the same estuary each year. There are several records of juveniles being recaptured in bays and estuaries other than those in which they were released. Two have gone from Port Phillip Bay to Westernport (Vic.), one from Port Sorell (Tas.) to the mouth of the Tamar River (Tas.), and another from Pittwater (Tas.)

to Norfolk Bay (Tas.). One of the sharks tagged in Port Phillip Bay and returned from Westernport in 1947 retained the plain backing disk but had lost the numbered fin tag. This shark was readily identified as coming from Port Phillip Bay because tagging in Victoria that year

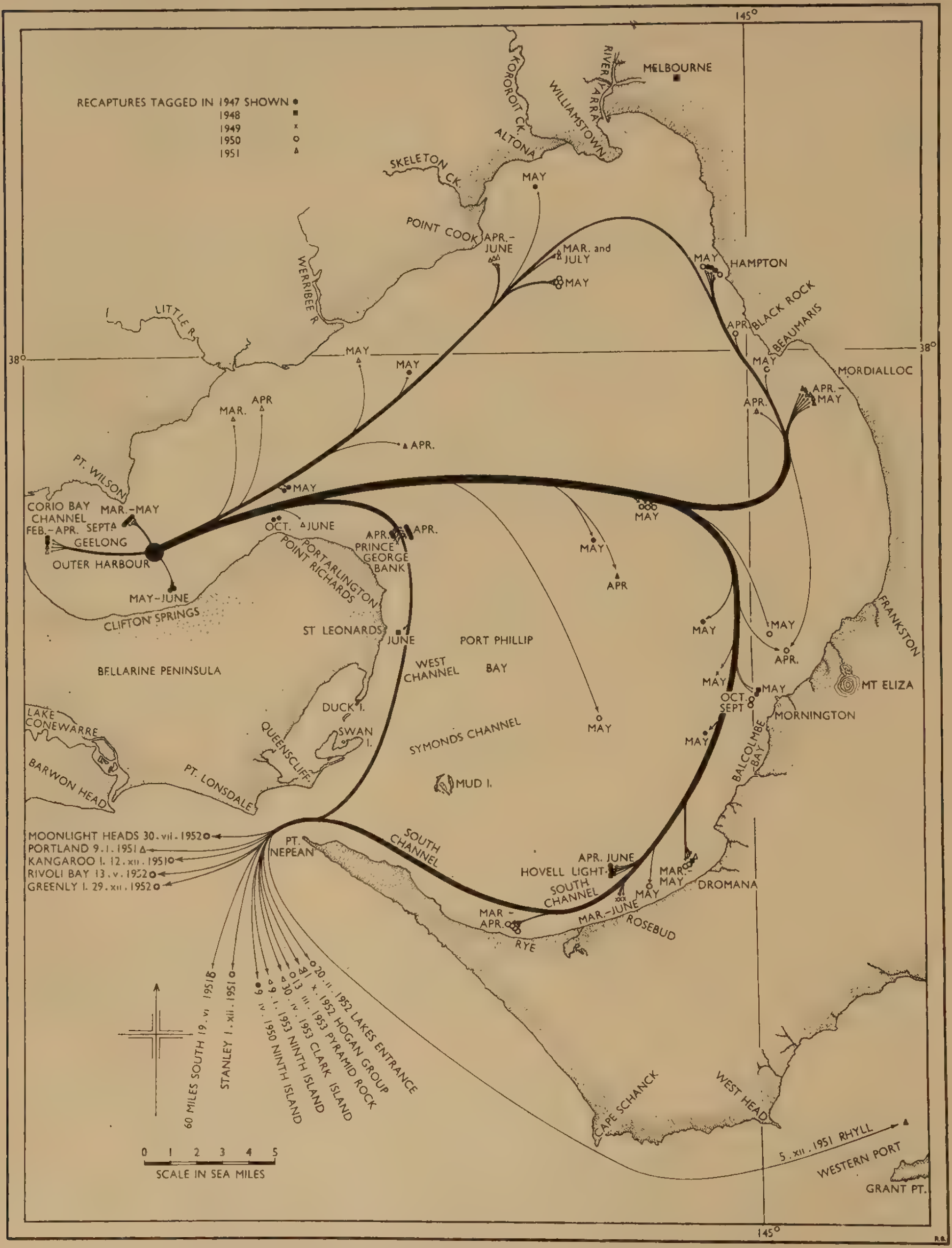
RECAPTURES TAGGED IN 1947 SHOWN ●
1948 ■
1949 ×
1950 ○
1951 ▲
MELBOURNE
RIVER YARRA
WILLIAMSTOWN
KOROROIT CK.
ALTONA
SKELETON CK.
POINT COOK
WERRIBEE R.
LITTLE R.
PT. WILSON
CORIO BAY
CHANNEL
FEB.-APR.
MAR.-MAY
SEPT.
GEELONG
OUTER HARBOUR
MAY-JUNE
CLIFTON SPRINGS
BELLARINE PENINSULA
LAKE CONEWARRE
BARWON HEAD
PT. LONSDALE
QUEENSCLIFF
DUCK I.
SWAN I.
ST LEONARDS
PORTARLINGTON
POINT RICHARDS
PRINCE GEORGE BANK
WEST CHANNEL
PORT PHILLIP BAY
SYMONDS CHANNEL
MUD I.
PT. NEPEAN
SOUTH CHANNEL
HOVELL LIGHT
RYE
ROSEBUD
DROMANA
BALCOMBE BAY
MORNINGTON
MT ELIZA
FRANKSTON
MORDIALLOC
BEAUMARIS
BLACK ROCK
HAMPTON
CAPE SCHANCK
WEST HEAD
WESTERN PORT
GRANT PT.
5.xii.1951 RHYLL
MOONLIGHT HEADS 30.vii.1952 ○
PORTLAND 9.1.1951 ▲
KANGAROO I. 12.xii.1951 ○
RIVOLI BAY 13.v.1952 ○
GREENLY I. 29.xii.1952 ○
60 MILES SOUTH 19.vi 1951 ■
STANLEY 1.xii.1951 ○
6.iv.1950 NINTH ISLAND
9.i.1953 NINTH ISLAND
30.iv.1953 CLARK ISLAND
13.iii.1953 PYRAMID ROCK
31.x.1952 HOGAN GROUP
20.ii.1952 LAKES ENTRANCE
38°
145°
0 1 2 3 4 5
SCALE IN SEA MILES
MAR. APR. MAY JUNE JULY SEPT. OCT.
MAR. and JULY
APR.-JUNE
APR.-MAY
MAR.-APR.
MAR.-JUNE
OCT. SEPT.
APR. JUNE

Fig. 13.—Main migration routes in Port Phillip Bay.

was confined to these two estuaries (Table 4) and this female was larger than either of the two males released in Westernport.

In Pittwater (Tas.) tagged sharks have been caught a month later 15-20 miles away. In the winter most juveniles have moved out of Pittwater into the deeper waters of Frederick Henry and Norfolk Bays since regular monthly sampling failed to catch them again until they returned in the following September and October. Often sharks caught during the spring had in their gut remains of fish whose habitat is restricted to kelp areas, the nearest being in Frederick Henry Bay about 15 miles away.

At St. Helens on George Bay (Tas.) there is a slightly modified behaviour pattern. Juvenile sharks spend as much as two successive years in this bay without making any seaward movement, probably because of its depth and good feeding grounds. George Bay has channels averaging 60 ft deep, while the shoals and flats carry a heavy *Zostera* growth. Consequently it provides shelter for a varied marine fauna such as small fish, crustaceans, and squid on which the young sharks feed. It is entirely different ecologically from the other estuaries sampled.

Very few sharks less than 1 yr old occur in this bay. The population consists of juveniles 45-70 cm in length with the larger sizes, 50-60 cm, predominating. Because of the number of double recaptures and the presence of juveniles throughout the year, it is evident that school sharks remain within this bay for about 2 yr. Sharks tagged during the summer have been recaptured at various times throughout the following year along with those tagged during the winter.

St. Helens yielded the best percentage return of any tagging centre, a total of 19 per cent. During the first 3 months of 1951 the number available for tagging was high but towards late autumn this dropped suddenly, as did the modal size of the remainder. Recruits from other areas would not be expected to enter the bay until the spring. From a sudden decrease in tag returns, the lower numbers caught, and their smaller size, it was concluded that the larger juveniles sampled over the previous 2 yr had left the bay.

It was expected that these larger migrating juveniles would reappear later in the commercial fishery, probably somewhere in the eastern Bass Strait area since the total lengths of sharks in the commercial catch in this part of the Strait average less than elsewhere (Appendix IV). In May 1952, one of these juveniles tagged in June 1950 was caught off Lakes Entrance, 170 miles north of St. Helens. The positions of this and other tag recoveries from inshore release centres are shown in Figure 14. As before, the lines show the general direction of the movement and the arrow-heads the position of each recovery.

These movements indicate a complete mixing of the populations from the various estuaries. In Figure 14 it can be seen that the 12 returns from eastern Bass Strait migrated from such widely separated estuaries as

Portarlington (Vic.), Port Sorell, St. Helens, and Gordon (Tas.), while it is obvious that the tagged shark caught near Eden, N.S.W. passed through these same waters. Further proof that juveniles in the open seas are not necessarily from nearby nursery estuaries or bays is given by the return of two tags from near Kangaroo I., S.A. They came from the two tagging centres furthest apart, namely, Pittwater and Portarlington. Other releases from these same centres have been caught near each other to the north-east of King I. and around Flinders I. (Appendix I).

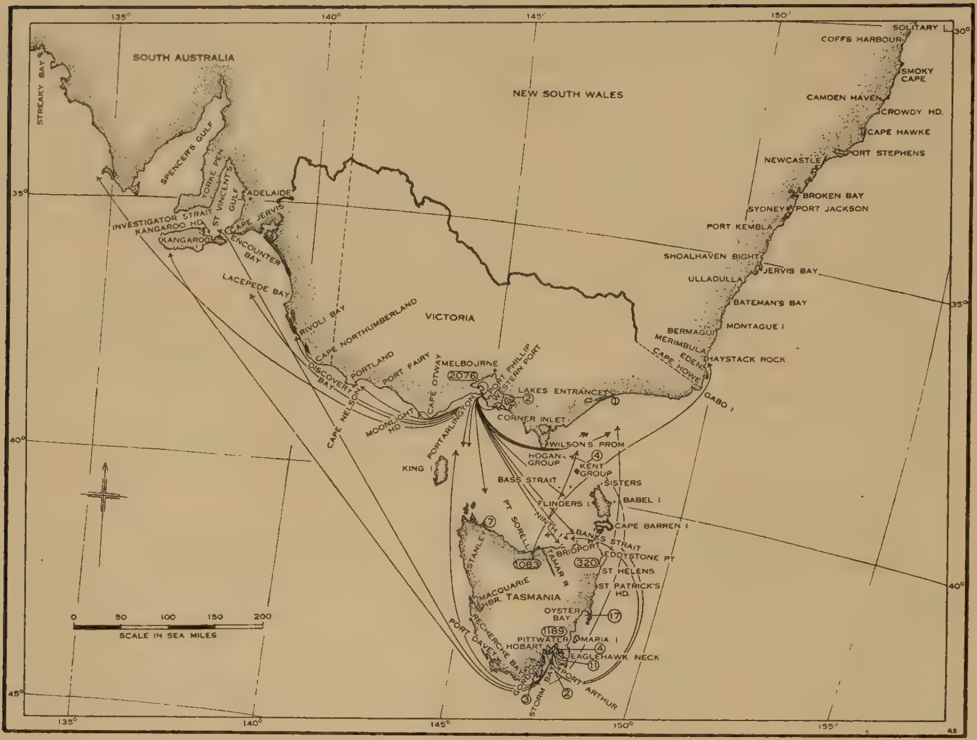
135°
140°
145°
150°
155°
30°
35°
40°
45°
SOUTH AUSTRALIA
STREAKY BAY
SPENCER'S GULF
YORKE PEN
ST VINCENT'S GULF
ADELAIDE
INVESTIGATOR STRAIT
KANGAROO HD
KANGAROO I
CAPE JERVIS
ENCOUNTER BAY
LACEPEDE BAY
RIVOLI BAY
CAPE NORTHUMBERLAND
DISCOVERY BAY
CAPE NELSON
PORTLAND
PORT FAIRY
MOONLIGHT HD
CAPE OTWAY
MELBOURNE
2076
PORT PHILLIP
WESTERN PORT
PORTARLINGTON
VICTORIA
NEW SOUTH WALES
LAKES ENTRANCE
CORNER INLET
WILSON'S PROM
HOGAN GROUP
KENT GROUP
KING I
BASS STRAIT
SISTERS
FLINDERS I.
BABEL I
CAPE BARREN I.
NINTH I
BANKS STRAIT
PT SORELL
STANLEY
TAMAR R
BRIDPORT
1083
320
EDDYSTONE PT
ST HELENS
ST PATRICK'S HD.
MACQUARIE HBR.
TASMANIA
OYSTER BAY
1189
PITTWATER
MARIA I
HOBART
EAGLEHAWK NECK
PORT DAVEY
RECHERCHE BAY
GORDON
STORM BAY
PORT ARTHUR
①
②
②
③
④
④
⑦
⑪
⑰
SOLITARY
COFFS HARBOUR
SMOKY CAPE
CAMDEN HAVEN
CROWDY HD.
CAPE HAWKE
PORT STEPHENS
NEWCASTLE
BROKEN BAY
SYDNEY
PORT JACKSON
PORT KEMBLA
SHOALHAVEN BIGHT
JERVIS BAY
ULLADULLA
BATEMAN'S BAY
MONTAGUE I
BERMAGUI
MERIMBULA
EDEN
CAPE HOWE
HAYSTACK ROCK
GABO I
0
50
100
150
200
SCALE IN SEA MILES

Fig. 14.—Migration of sharks tagged at inshore centres.

The Kangaroo I. recapture of a male (585 mm) recorded the longest direct surface distance (700 miles) yet traversed by such a small juvenile although it was not the first time that a tagged shark from Pittwater had been recaptured there. In June 1951, a large tagged female was caught at Kangaroo Head, Kangaroo I., 18 months after she had released her young in Pittwater; and the above juvenile, released a year later, was hooked after a similar period of freedom, only 50 miles further west along the same coast.

The small size of the five tagged juveniles recovered in South Australian waters prompted comment from the fishermen catching them. In 1951, the South Australian shark fishermen first encountered small sharks in their catches whereas previously they had only caught adults. The juvenile Pittwater return from Kangaroo I. was the smallest school shark ever caught by the experienced professional fisherman who recovered it. No such comment about the small size of recaptured tagged sharks has been passed by fishermen operating in eastern Bass Strait, who have always fished a smaller size of sharks than elsewhere.

Fishing tests around the Furneaux Group and sampling of commercial catches in the eastern Bass Strait area have shown that waters of this extensive region support a population of juvenile sharks of sizes larger than those encountered in the estuaries yet smaller than those in western Bass Strait. Evidence from tagging supports the theory that by far the greater proportion of juveniles migrating from the estuaries move towards the wide extension of the continental shelf in eastern Bass Strait, where they spend a further period of their life. The proportion of immature sharks in the commercial catches in this area is higher than elsewhere. The entry of the smaller sharks into this area has little or no effect on the population or its modal sizes since this is counterbalanced by the departure of the larger sharks from the area. Evidence in support of this theory is shown by the recapture in this area of tagged sharks from various estuaries and the subsequent recapture in widely scattered locations of sharks released around Flinders I. (Fig. 15). Also it is believed that the immature sharks from Portarlington and Pittwater caught near the north-eastern Tasmanian coast were from the eastern Bass Strait population. The South Australian and western Bass Strait recaptures of sharks released at Portarlington and Pittwater may be considered as examples of the larger immature sharks which occasionally frequent islands and open coastal areas. Those caught in the latter area may have been moving eastwards, for there is a somewhat haphazard migration into the eastern Bass Strait region.

(*b*) *Off-shore Tagging*

The number of sharks tagged and the recaptures for each off-shore position are given in Appendices II and III. In Figure 15 the circled figures represent the total number of sharks tagged and released at each position, and as before the arrow-head indicates the position of recapture, and the lines the general direction of the movement away from the tagging position.

Like the juveniles, the adults undertake extensive migrations which serve to demonstrate how complete is the mixing of this homogeneous stock. The movements of sharks in Bass Strait are much better known than elsewhere because in these waters the intensity of fishing is greatest and consequently the tag returns are higher.

As can be seen from Figure 15, there are several tagging positions from which sharks have migrated in many different directions. Seven centres with multiple returns had at least two recoveries (two had three

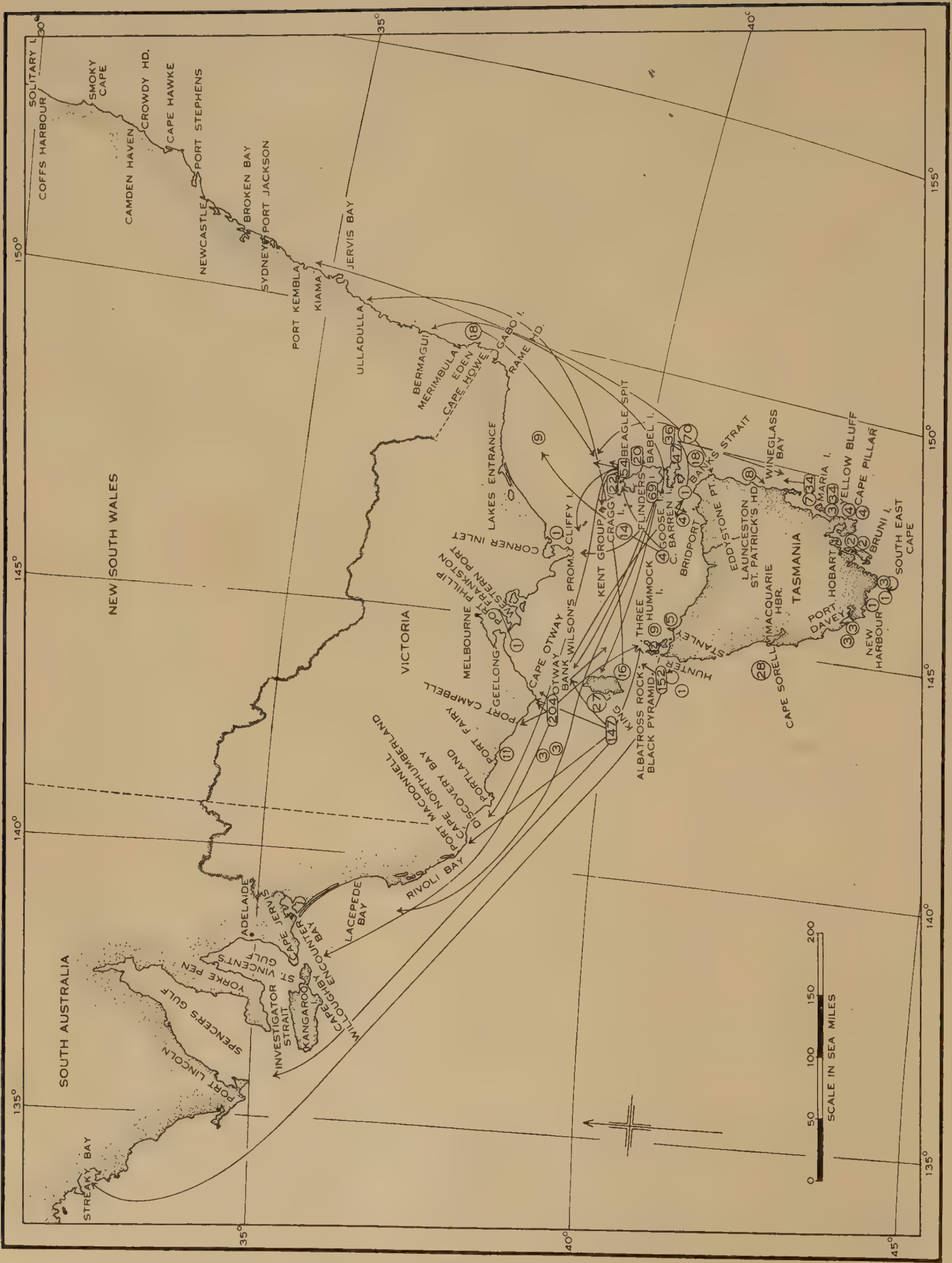
SOUTH AUSTRALIA
NEW SOUTH WALES
VICTORIA
TASMANIA
SOLITARY I.
COFFS HARBOUR
SMOKY CAPE
CAMDEN HAVEN
CROWDY HD.
CAPE HAWKE
PORT STEPHENS
NEWCASTLE
BROKEN BAY
PORT JACKSON
SYDNEY
PORT KEMBLA
KIAMA
JERVIS BAY
ULLADULLA
BERMAGUI
MERIMBULA
EDEN
CAPE HOWE
GABO I.
RAME HD.
LAKES ENTRANCE
CORNER INLET
WESTERN PORT
FRANKSTON
PORT PHILLIP
MELBOURNE
GEELONG
CAPE OTWAY
OTWAY BANK
WILSON'S PROMY.
CLIFFY I.
KENT GROUP
CRAGGY I.
BEAGLE SPIT
BABEL I.
FLINDERS I.
GOOSE I.
C. BARREN I.
BANKS STRAIT
THREE HUMMOCK I.
HUNTER I.
ALBATROSS ROCK
BLACK PYRAMID
KING I.
STANLEY
BRIDPORT
EDDYSTONE PT.
LAUNCESTON
ST. PATRICK'S HD.
WINEGLASS BAY
MARIA I.
YELLOW BLUFF
CAPE PILLAR
HOBART
BRUNI I.
SOUTH EAST CAPE
NEW HARBOUR
PORT DAVEY
MACQUARIE HBR.
CAPE SORELL
PORT CAMPBELL
PORT FAIRY
PORTLAND
DISCOVERY BAY
CAPE NORTHUMBERLAND
PORT MACDONNELL
RIVOLI BAY
LACEPEDE BAY
ADELAIDE
CAPE JERVIS
ENCOUNTER BAY
ST. VINCENT'S GULF
YORKE PEN
KANGAROO I.
INVESTIGATOR STRAIT
CAPE WILLOUGHBY
SPENCER'S GULF
PORT LINCOLN
STREAKY BAY
30°
35°
40°
45°
135°
140°
145°
150°
155°
18
9
1
22
54
14
20
36
70
47
69
18
4
1
8
7
34
3
34
4
4
2
2
3
1
1
3
3
5
9
152
1
16
27
147
204
3
3
11
1
28
0
50
100
150
200
SCALE IN SEA MILES

Fig. 15.—Migration of tagged sharks from off-shore positions.

recoveries) from releases made the same day. The longest and also the least distances travelled were recorded by sharks released together at the Black Pyramid (Appendix II). The longest direct distance, approx. 750 nautical miles, was covered in 9 months, whereas the shark which apparently failed to migrate was free for almost 3 yr.

The two recoveries from near the northern limits of the fishery, one near the head of the Bight and the other from Ulladulla, N.S.W. recorded the longest distances travelled by school sharks. One went from the Black Pyramid to Streaky Bay, S.A., and the other from the east side of King I. in western Bass Strait to Ulladulla, approx. 500 miles. Another long movement northwards was that of the shark, free for 63 wk, recaptured at Kiama, N.S.W. about 50 miles north of the Ulladulla return. It had been released at the south-eastern entrance to Bass Strait on the same day as the shark which was caught in the opposite direction, near Eddystone Point (Tas.), after a further 36 wk of freedom. At an adjacent centre two sharks were tagged which both made southerly movements before recapture. The movement of one of these (tag No. 2245) was of particular interest, for after being hauled from 180 fm, tagged, and released again, it was in very good condition when recaptured in 80 fm off Maria I. over 2 yr later.

The other recapture of an adult shark in southern Tasmanian waters was made off South Cape and although this shark had been free for 2 yr it was caught only 5 miles from where it was released. It is possible that this shark had migrated only to return to be caught again nearby.

Shark fishing off the exposed west coast of Tasmania is limited, owing to distances from market and lack of suitable shelter from the bad weather. Therefore because of the nature of this spasmodic fishing it will be extremely difficult to determine whether school sharks from southern Tasmanian waters migrate northwards along the west coast of the island to reach Victorian and South Australian waters, but since school sharks occur in these west coast waters it is logical to assume that they can also migrate along this coast.

From a recapitulation of the tagging results, supplemented by reference to port catch statistics, observations on fishermen's catch returns, and fishing operations of the research vessel, it has been possible to determine the general migration pattern of school sharks. The following account is a composite one pieced together from data derived from the above sources and supplemented by anecdotal evidence gleaned from professional shark fishermen.

(*c*) *General Migration Pattern*

During the late spring and early summer months the adult females move into, and give birth to their young in, the shallow waters of protected bays and certain estuaries of the south-eastern Australian coast. After the liberation of their young, they leave these "nursery" areas and begin active foraging to replenish the reserve food resources which were stored in the liver and were depleted during the period of gestation. The young remain in these "nursery" areas until the late summer months, when they begin their leisurely seaward movement to deeper coastal waters where they stay over the winter. In the following spring the majority return to their former "nurseries" whilst others move to adjacent estuaries and bays. Those juveniles, 2 yr and older, which do not return to the estuaries but adopt the open sea existence, tend to move towards the area of eastern Bass Strait where the bulk of the immature stock of school sharks is centred. Others remain in off-shore areas, attaching themselves to foraging schools.

In the late summer and winter months the adult school sharks, which during the summer were distributed within the limits of the continental shelf, either move toward the edge of this shelf (70-100 fm) or else migrate into the warmer waters of South Australia and New South Wales. The return movement from these northern waters commences about October or November. The sharks which move out to the edge of the continental shelf, where copulation takes place in May and June, disperse in these deep waters by July or August. About 2 months later they begin their leisurely return movement and by November have reached the shallower inshore waters. Superimposed on this main movement is the purposeful migration to nursery areas of the gravid females to release their young. Towards the end of November the sharks spill through the four entrances into Bass Strait and spread throughout its waters, whereas elsewhere there is a random diffusion of schools of sharks throughout the shallower waters in search of food.*

During the time the sharks travel together, new recruits join the school as older members leave it. This explains the wide dispersal of members of the schools tagged at the same time and also accounts for the fairly uniform sizes of fish within the school. Additional evidence in support of this theory about the composition of schools is shown by the occasional presence of darkly coloured individuals among the catch of uniformly lighter-coloured sharks of the same school. Sharks require a day or so before they show a colour adaptation to their immediate surroundings (Parker 1937) and therefore the presence of some darkly coloured individuals in a school of lighter-coloured sharks has been interpreted as representing some very recent recruits to that school. During fishing operations it has been observed that darker individuals came from heavy reef bottom whereas the lighter ones frequented open or "coral" bottom feeding grounds.

This recapitulation of the general movement of school sharks in the waters of south-eastern Australia deals with the bulk of the stock of sharks, though it is realized that in specific places variations from the general behaviour will be found. In the whole area over which the sharks are caught, the only relatively untouched region is that on the west coast of Tasmania which serves as a small reservoir feeding western Bass Strait. Now that deep long-line fishing has commenced, the small unfished part of the shark stock located over the edge of the shelf will be further exploited and the whole of the stock fished over almost its entire range.

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* Since this paper was submitted for publication further tag returns have been received confirming this theory of the migration pattern.

VI. Rate of Growth

Because of the inherent difficulty in obtaining satisfactory data for determining the rate of growth of elasmobranchs this aspect of their biology has received very little attention. They have no suitable otoliths and the scales, so far, have proved unsatisfactory for age determination. However, Kaganovskaia (1933, 1937), quoted by Bonham *et al.* (1949), has shown for the Pacific dogfish *Squalus suckleyi* from the seas of Japan and Okhotsk that, within certain limits, the annulations of the spine of the posterior dorsal fin may be used as a possible means of assessing its age, and this observation was confirmed by them on the rate of growth of this dogfish in the waters of the State of Washington.

Templeman (1944) applied the method of differential growth increments to derive a curve showing the rate of growth of the Atlantic spurdog, *Squalus acanthias*, while Desbrosses (1938) attempted to determine the rate of growth of the six-gilled shark, *Hexanchus griseus* (Bonnaterre 1788) Rafinesque 1810, by the Petersen method with an extremely small number of specimens. Jacups (1943) reported on the growth of the crested Port Jackson shark, *Molochophrys galeatus* (Günther), held in an aquarium and these observations were later extended and reported by Whitley (1949). In the present investigation the age of sharks was determined by the Petersen method supplemented by an extensive tagging programme from which was derived the rate of growth and age at sexual maturity of the Australian school shark. The results from tagged sharks indicate that there is no seasonal slowing down of growth.

The total lengths used in the preparation of the Petersen length frequency graph were limited to those taken within a 4-month period from mid November to mid March from all sources over 6 yr. Partial lengths obtained from dressed carcases were converted to total lengths by regression equations (least squares method) derived from an extensive series of partial and total length measurements of whole sharks. Growth was shown to be isometric (Fig. 16).

The regression formulae for converting partial lengths to total lengths were:

Fifth gill slit to tip of tail:

$$Y = 1.2x + 2.8,$$

Tip of nose to base of caudal fin:

$$Y = 1.2x + 6.3,$$

where x = partial length and Y = total length.

The period between mid November and mid March was selected as being the most suitable for an age analysis by the Petersen method, for, depending on latitude and environmental conditions in the "nursery" areas, most young sharks are born by the end of December. It was also essential to assign an arbitrary time as the birthday of juvenile sharks and January 1 was selected as best fitting the collective data.

It has been found that females release their young in Port Sorell as much as 4 wk earlier than in the estuaries of southern Tasmania. Therefore as these juveniles in the Bass Strait nursery areas are as much as a month older than those in the south it would be expected that initially their modal or mean length would be greater than those from the southern estuaries. However, as shown in Figure 11 this size difference may not always exist if, as often occurs, the mean size of the females in the southern areas is greater. If this size difference is present, these chance variations are soon obscured by the mixing of migrating estuarine populations. With adequate mixing the size range within an age-group would tend towards a normal distribution.

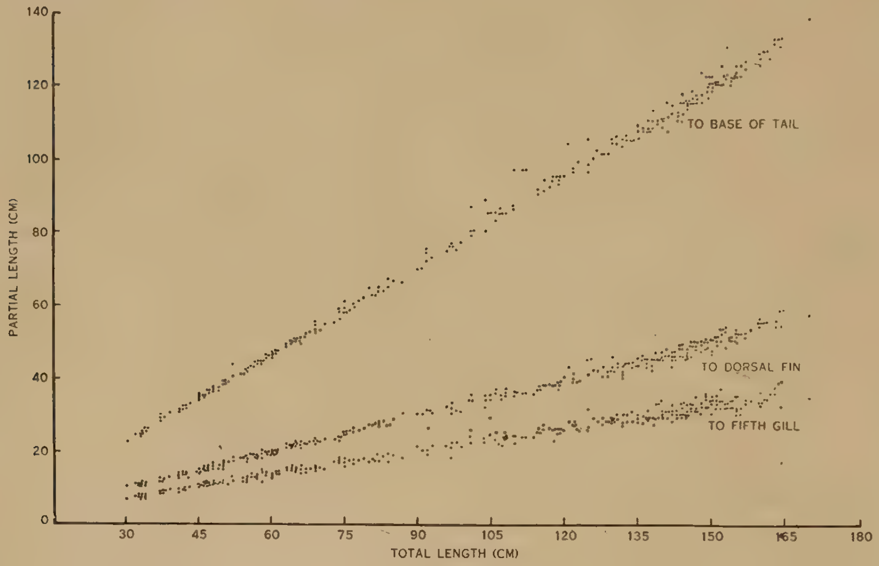

Fig. 16.—Relationship between total and partial lengths of school sharks.

In determining the age of school sharks, firstly it was necessary to prove conclusively that each of the modes in a length frequency graph represented a year group, and secondly, having proved this assumption, to identify each modal length with its year group. It was by this line of reasoning that the ages of sharks were determined and from these data the growth rate curve was derived.

In Figure 12 the modes of the length frequency curves prepared for both sexes of 941 full-term embryos are shown to be identical, namely

300 mm, and from these results and measurements of developing embryos it is deduced that the intra-uterine rate of growth of both sexes is similar. Shortly after birth there is still no difference in the mean lengths of the two sexes (320 mm in January) nor can any difference in mean lengths be detected within samples collected together over the size range of this species. There is no significant difference between the mean monthly growth increments in the different size-groups of male and female tagged sharks (Table 5) and on this evidence the rate of growth is taken to be the same for both sexes. Consequently there is no need to separate the sexes in growth rate studies. Steven (1936) found no difference in the growth rates of the two sexes of the thornback ray (*Raia clavata* L.) and Templeman (1944) was unable to find any between the sexes in *Squalus acanthias*.

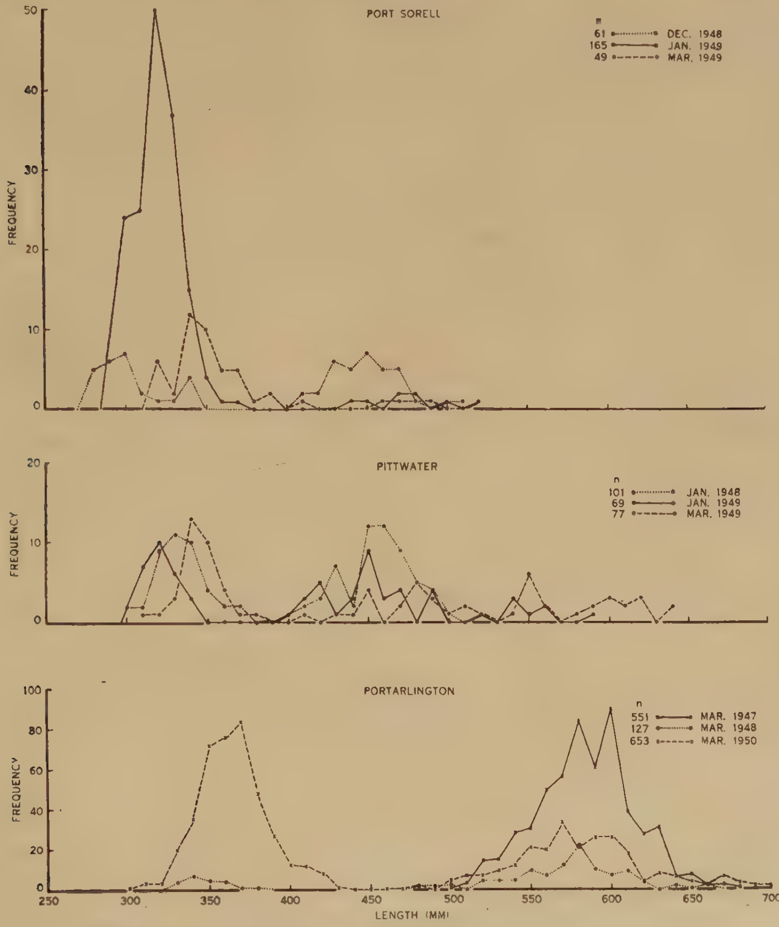

Fig. 17.—Length frequency curves for juvenile sharks in certain estuaries.

Measurements of both sexes were combined to prepare the length frequency curves for the three estuarine populations of Portarlington, Pittwater, and Port Sorell (Fig. 17). These curves show that although sharks with a modal length of approximately 450 mm are missing from Portarlington they are always present in Pittwater and occasionally at Port Sorell. The regular monthly sampling of the juvenile populations in these two estuaries soon showed that the modal length of the sample increased by approximately 10 mm per month. If this increment of 10 mm per month is taken as representing the mean monthly length increase of a random sample of 0+ juvenile population then on their first birthday they should be about 450 mm in length, assuming a modal length of 320 mm at birth on January 1. Therefore in any length frequency curve which includes the 1+ juveniles there should be a mode at 450 mm. Such a mode is present consistently only in the Pittwater samples, indicating that at least the 0+ and 1+ yr groups frequent this estuary. Occasional specimens of this 1+ group are caught in the other estuaries where the average monthly increases in length are identical with those from Pittwater and so justify the conclusion based on monthly length increments that sharks with a mean or modal length of 450 mm in January are 1 yr old. This size-group is almost completely absent from the Portarlington area.

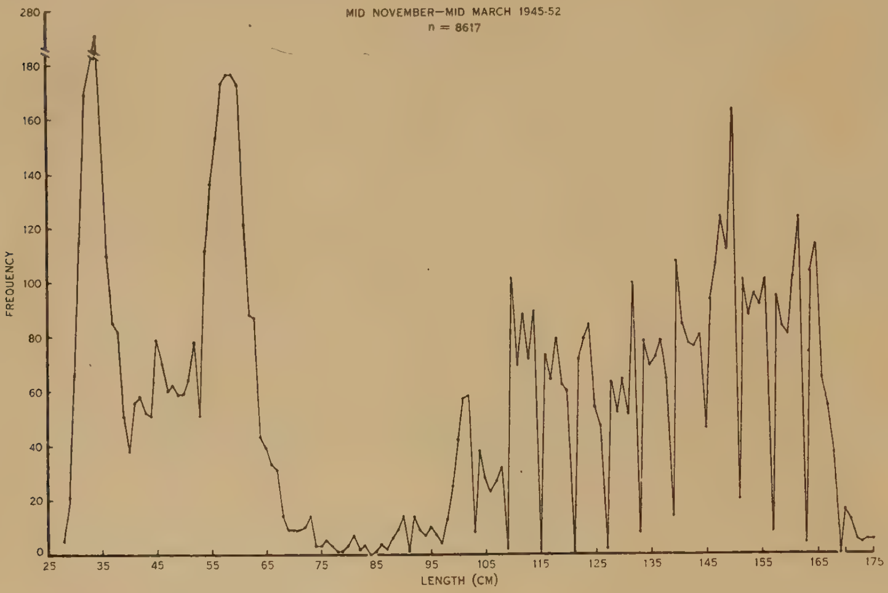

Fig. 18.—Composite length frequency curve for all sizes of school sharks.

Since recently born juveniles have a modal length of 320 mm in January and sharks 1 yr old have a mean or modal length of 450 mm, then it would be expected that juveniles from Portarlington with a modal length of 580 mm would be 2 yr old. Tagging results and monthly sampling have confirmed this supposition (Table 9).

If reference is now made to the composite length frequency graph (Fig. 18), prepared from over 8600 measurements, it will be seen that the first three modes lie at 34, 45, and 58-59 cm.

These values vary from those derived for the January modal lengths of 32, 45, and 58 cm. The increase from 32 to 34 and 58 to 59 cm is due to the time of collection, most of the measurements having been taken in the last half of the 4-month period. Measurements of most of the remaining size-groups have been more evenly distributed over the selected period. Where one or two secondary modes occur in the same group these are probably due to the presence of two or three large separate samples taken at evenly spaced intervals over the 4-month period and have not invalidated the determination of the year-group for that size range. The highest mode has been taken as representing the modal length of that particular year group.

The modes lying between 59 and 102 cm are small, and as a consequence there is some doubt about their significance as indicators of age-groups. However, the data derived from the monthly growth increments of 18 (1+ yr) and 35 (2+ yr) sharks returned after periods varying from 3 to 160 wk have shown that the mean monthly increment of the 1+ sample is 10.5 mm and that of the 2+ sample is 8.97 mm (Table 5). Hence the modal length of 3-yr-old sharks calculated from this data could be expected to be about 70 cm. Likewise the seven returns in the next group, assumed to represent the 3+ sharks, indicate a growth rate comparable to that for the 1+ and 2+ yr groups and thus the modal or mean length of sharks in the next year group could be expected to be about 81 cm. This calculated mean or modal length confirms the significance of the small mode at 81 cm as representing the mode for the 4-yr age-group. The possibility that the mode at 90 or 92 cm is the modal length of 5-yr sharks is confirmed by tag returns. The tagged shark *A*58 (Table 9) during 160 wk of freedom grew from 589 mm (almost the modal length of 2-yr sharks) to 950 mm. In that shark the January modal length would be less than 95 cm as it was caught in April. The January modal length is assumed therefore to be at 92 cm rather than at 90 cm. Data from the two returns in the 5-yr group (Table 9) give support to the selection of 92 cm as the modal length of 5-yr-old sharks.

Extending this interpretation of the modal lengths it can be seen that 6-yr-old sharks have a modal length of 102 cm and the appropriate age-groups for the following modal or mean lengths are:

110 cm	7 yr	132 cm	10 yr
118 cm	8 yr	137 cm	11 yr
124 cm	9 yr	140 cm	12 yr

TABLE 9
MONTHLY INCREMENTS OF TAGGED SCHOOL SHARKS

Tag No.	Sex	Date Released	Locality	Length at Release (mm)	Length at Recapture (mm)	Length Increment (mm)	Weeks of Freedom	Condition	Average Monthly Increment (mm)
1 + Yr Group									
*A*426	F	24.iii.47	Portarlington	517	530	13	6.5	Dead	8.0
*A*1260	F	8.xii.48	Port Sorell	432	441	9	6.3	Alive	5.7
*A*2684	F	10.x.49	St. Helens	425	565	140	76.3	Alive	7.3
*A*1250	M	8.xii.48	Port Sorell	468	488	20	6.8	Alive	11.7
*A*1300	M	12.i.49	Pittwater	490	500	10	3	Alive	13.3
*A*2692	F	11.x.49	St. Helens	465	485	20	9.3	Alive	8.6
*B*5627	M	16.ii.50	Pittwater	450	451	1	3.6	Alive	1.1
*B*6724	F	29.iii.50	Port Sorell	448	635	187	75.4	Dead	9.9
*B*6907	F	26.viii.50	St. Helens	485	624	139	38.7	Dead	14.4
*B*6917	M	27.viii.50	St. Helens	500	553	53	15.8	Alive	13.4
*B*6967	F	14.xii.50	St. Helens	478	600	122	26.6	Dead	18.3
*B*7603	F	23.i.51	St. Helens	515	557	42	9.1	Alive	18.5
*B*7612	M	23.i.51	St. Helens	500	567	67	17.3	Dead	15.5
*B*8057	F	16.iii.51	Portarlington	472	514	42	15.7	Dead	10.7
*B*8078	M	16.iii.51	Portarlington	425	533	108	52	Dead	8.3
*B*8235	F	17.vi.51	St. Helens	470	530	60	30.8	Dead	7.8
*B*8453	F	18.xii.51	St. Helens	490	505	15	5	Dead	12.0
2811	F	19.viii.51	St. Helens	462	475	13	12.4	Dead	4.2
2 + Yr Group									
*A*58	F	15.iii.47	Portarlington	589	950	350	160.1	Dead	8.7
*A*195	M	15.iii.47	Portarlington	560	581	21	9	Dead	9.3
*A*214	F	16.iii.47	Portarlington	603	619	16	10.3	Dead	6.2
*A*5304	F	12.i.49	Pittwater	565	576	11	3	Alive	14.6
*A*1325	M	28.ii.49	Portarlington	600	613	13	6.5	Alive	8.0
*A*5177	M	10.i.50	Pittwater	535	952	417	164.4	Alive	10.1
*A*5308	M	10.i.50	Pittwater	565	825	260	130.4	Alive	7.9

TABLE 9 (*Continued*)

Tag No.	Sex	Date Released	Locality	Length at Release (mm)	Length at Recapture (mm)	Length Increment (mm)	Weeks of Freedom	Condition	Average Monthly Increment (mm)
				2 + Yr Group (*Continued*)					
*B*5687	F	20.ii.50	St. Helens	580	600	20	8.7	Alive	9.2
*B*5758	F	1.iii.50	Portarlington	560	825	265	128.8	Dead	8.2
*B*5803	F	1.iii.50	Portarlington	600	650	50	26.7	Dead	7.5
*B*5845	M	1.iii.50	Portarlington	585	597	12	9	Dead	5.3
*B*5892	M	1.iii.50	Portarlington	600	950	350	126	Dead	11.1
*B*6006	F	3.iii.50	Portarlington	580	762	182	67.6	Dead	10.7
*B*6648	M	23.iii.50	St. Helens	585	600	15	11.8	Alive	5.1
*B*6649	M	23.iii.50	St. Helens	600	640	40	29.5	Dead	5.4
*B*6652	M	23.iii.50	St. Helens	605	640	35	17.7	Alive	7.9
*B*6655	F	24.iii.50	St. Helens	565	600	35	22.3	Alive	6.3
*B*6659	M	24.iii.50	St. Helens	610	740	130	52.7	Dead	9.8
*B*6675	M	25.iii.50	St. Helens	550	597	47	25.8	Dead	7.3
*B*6677	F	25.iii.50	St. Helens	578	650	72	27.6	Dead	10.4
*B*6975	M	15.xii.50	St. Helens	551	606	55	14.7	Alive	14.9
*B*6977	F	15.xii.50	St. Helens	532	601	69	23.3	Dead	11.8
*B*7519	F	15.xii.50	St. Helens	560	629	69	23.8	Dead	11.6
*B*7575	M	10.i.51	Pittwater	600	775	175	93.6	Alive	7.5
*B*7606	F	23.i.51	St. Helens	580	628	48	17.3	Alive	11.1
*B*7609	F	23.i.51	St. Helens	545	582	37	25.7	Dead	5.7
*B*7614	M	23.i.51	St. Helens	565	570	5	4.3	Alive	4.6
*B*7617	F	23.i.51	St. Helens	565	583	18	6.3	Alive	11.4
*B*7671	F	22.ii.51	St. Helens	550	580	30	8.3	Alive	14.4
*B*7674	M	22.ii.51	St. Helens	570	628	58	13	Dead	17.8
*B*7745	M	14.iii.51	Portarlington	632	700	68	43	Alive	6.3
*B*7852	F	14.iii.51	Portarlington	618	838	220	80.8	Alive	10.9
*B*8136	F	27.iii.51	St. Helens	572	597	25	29.8	Alive	3.4
*B*8160	F	28.iii.51	St. Helens	585	595	10	8.1	Dead	4.9
*B*8218	M	24.v.51	St. Helens	622	669	47	21.5	Alive	8.7

TABLE 9 (*Continued*)

Tag No.	Sex	Date Released	Locality	Length at Release (mm)	Length at Recapture (mm)	Length Increment (mm)	Weeks of Freedom	Condition	Average Monthly Increment (mm)
					3 + Yr Group				
*A*1999	F	2.x.49	Goose I.	700	1126	526	164	Dead	12.8
*B*6049	F	5.iii.50	Portarlington	675	690	15	6.1	Dead	9.8
*B*6900	F	26.viii.50	St. Helens	642	710	62	21.4	Dead	11.6
*B*7521	M	15.xii.50	St. Helens	664	729	65	23.1	Alive	11.2
*B*7615	M	23.i.51	St. Helens	705	710	5	6.3	Alive	3.2
*B*7734	F	14.iii.51	Portarlington	650	756	126	80.8	Alive	6.2
*B*7809	F	14.iii.51	Portarlington	665	939	274	95.3	Alive	11.5
					4 + Yr Group				
*A*970	F	21.ii.48	Portarlington	810	825	15	5.7	Alive	10.5
*B*5975	F	2.iii.50	Portarlington	760	1054	294	102.6	Alive	11.5
					5 + Yr Group				
*B*6288	M	13.x.50	Goose I.	840	1160	320	122.1	Alive	10.6
*B*6955	F	8.xi.50	Pittwater	865	1026	161	111.7	Alive	5.7
					Adult Sharks				
*B*6106	F	14.iv.50	Otway Bank	1200	1383	183	146.4	Dead	5.0
*A*2192	M	3.xii.49	Otway Bank	1240	1320	80	122.4	Dead	2.6
*B*6105	F	14.iv.50	Otway Bank	1250	1338	88	103.1	Dead	3.4
*B*7013	M	17.vii.51	Cape Barren I.	1330	1370	40	77.4	Dead	2.06
*B*6468	M	2.iv.51	King I.	1350	1350	—	74.6	Dead	—
*A*2245	M	15.xii.49	Flinders I.	1380	1430	50	120	Dead	1.66
*B*6436	M	7.iii.51	East Banks Strait	1410	1448	38	104.1	Dead	1.44
236	F	6.vi.49	Black Pyramid	1470	1515	45	151.3	Dead	1.2
*B*6204	M	30.iv.50	Beagle Spit	1490	1524	34	131	Dead	1.03
*B*6416	F	13.xii.50	Goose I.	1500	1560	60	93.1	Dead	2.57
*B*6559	F	18.iv.51	East Banks Strait	1510	1570	60	63	Dead	3.8

The determination of the age-group from modes to 140 cm has been relatively straightforward but beyond this modal length it becomes more difficult. Above 120 cm the smallest males become sexually mature, as do the smallest females above 135 cm (Section IV(*h*)). In animals of indeterminate length, such as fish, it is well known that there is usually a progressive slowing down in the rate of growth with increasing age (Thompson 1942) and therefore as these sharks approach maturity their annual growth increments would be expected to decrease. The falling off in rate of growth would not be sudden but would take place gradually, and above the modal length of 140 cm it is not expected that the next age-group of 13 yr would have a modal length of 150 cm. If it is assumed that 150 cm is the modal length of the 13-yr age-group, then it would mean a sudden increase in rate of growth from 3 to 10 cm/yr. This is most unlikely and therefore it is essential to interpret with caution the age of sharks after both sexes reach sexual maturity. The modes of such groups with very small annual increments would tend to become closer until finally these modes would be almost indistinguishable from each other. It is believed that this occurs with the modal groups above 140 cm.

TABLE 10

MODAL LENGTHS AND ANNUAL GROWTH RATES

Age-group (yr)	Modal Length (cm)	Annual Increment (cm)	Age-group (yr)	Modal Length (cm)	Annual Increment (cm)
1	45	13	7	110	8
2	58	13	8	118	8
3	70	12	9	124	6
4	81	11	10	132	8
5	92	11	11	137	5
6	102	10	12	140	3

By examination of the annual increments of school sharks for the first 12 yr, taking the modal lengths already derived (Table 10), it can be seen that the last annual increment is 3 cm. If, however, the mean monthly increment of 11 tagged sharks whose lengths ranged from 125 to 151 cm (Table 9) was only 2.25 mm (annual 2.7 cm) then the derived figure of 3 cm from the length frequency polygon is reliable, and there should be three and possibly four successive age-groups within the size range 140-150 cm. By following the same reasoning that the annual growth increment is decreasing, there should be at least two and possibly three age-groups within 150-156 cm and likewise two or three age-groups within 156-162 cm.

The assumption that there are four age-groups within 140-150 cm, and three each within the 6-cm range in the larger sizes, is confirmed by comparing the curve drawn through these points with the slopes of the growth rates for the 11 adult tagged sharks (Table 5). The curve so drawn through the points at 140 cm for 12 yr, at 150 cm for 16 yr, at 156 cm for 19 yr, and at 162 cm for 22 yr, has the same slope as those prepared for tagged sharks *B*6105, *B*6106, and *B*7013, a steeper slope than *A*2192, *B*6204, *B*6436, 236, and *A*2245, and only slightly flatter than *B*6416 and *B*6559 (nil for *B*6468). A curve based on three year-groups between 140 and 150 cm and another four to 162 cm would have given a very unsatisfactory fit to the data. In February 1952, a mature 94-cm *Squalus suckleyi*, released in North American waters in 1944, was caught off Honshu in northern Japan and during its extensive period of freedom had grown very little. Its migration of 5000 miles was the longest yet recorded for any fish. Another tagged dogfish, an immature female of 64.7 cm, grew only 14.2 cm after nearly 8 yr of freedom (Fish. Res. Bd. Canada, Prog. Rep. Pac. No. 92). Such concrete evidence from tagging other elasmobranchs of their slow rate of growth gives additional support to the argument above about the slow growth of school sharks after they reach sexual maturity.

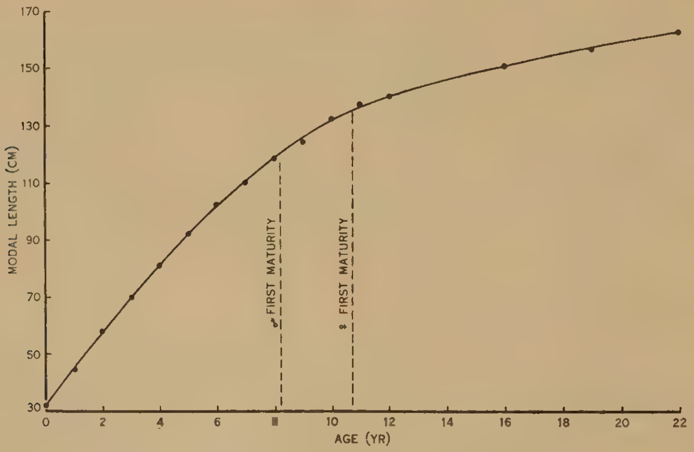

Fig. 19.—Growth rate curve of school sharks.

By plotting the modal length in centimetres (x) against the time in years (y) and drawing a smoothed curve through these points, assuming 10 age-groups within the range 140-162 cm, a growth rate curve for school sharks has been derived.

Since 120 cm is the smallest size at which the male school sharks become mature (Section IV(*h*)) such males are over 8 yr old, though the majority which mature later would not reach this state until at least the following year, when they would be 9 yr old. Likewise the smallest female which reaches sexual maturity at 135 cm would be over 10 yr old. It is possible that they would not bear young that year, for the eggs are usually not ovulated until about May and June of each year and therefore the average female would be at least 11+ yr before she was capable of reproduction. Consequently her first brood of young would not be produced until her twelfth birthday, as the gestation period is approx. 6 months. Because the size at first maturity is more definite than either 50 per cent. or complete maturity in both sexes, it is taken that the smallest males become mature at 8 yr and the smallest females at 10+ yr, their first brood being produced the following year.

The times taken to reach sexual maturity in the two sexes are not unduly long. Steven (1936) calculated on the basis of annual increments of 6 cm in the disk width of the thornback ray (*Raia clavata* L.) that the male reached maturity in 7 yr, the female in "another two years or so". Templeman (1944) estimated that the male of the Atlantic dogfish (*Squalus acanthias*) reached maturity in 5-6 yr, the female in 7-8 yr. The crested Port Jackson shark, *Molochophrys galeatus,* kept alone in an aquarium, laid its first eggs 11½ yr after its birth (Whitley 1949). Desbrosses (1938) considered that the large six-gilled shark, *Hexanchus griseus* Rafinesque, became adult in 5-6 yr, although he stated that his data were rather meagre. In view of the evidence produced for other elasmobranchs the figure of 5 yr from birth to female sexual maturity for such a large shark would seem unduly short.

(*a*) *Post-Mortem Alterations in Length*

Some of the variation in the individual growth rates may be due to post-mortem changes in the length of sharks before they were measured. It had been found that sharks, carefully measured whilst alive and again after death, had altered in total length (Tables 11 and 12). This alteration in length was most irregular and occurred after death in either air or water. After passing through an indefinite period of *rigor mortis,* the body became limp and it was during these different post-mortem stages that alterations in length were most evident. Freezing and subsequent thawing also caused unpredictable changes in the total length.

Because of these alterations in length after death tagged sharks should be measured as soon as possible after recapture and the condition of the shark recorded. None of the juvenile tagged sharks which exhibited nil or negative growth was listed in Table 9. All doubtful returns were omitted from this table for the reasons given above and against each return recorded was stated the condition of the shark when it was measured. No explanation can be offered for these observed facts but it was desirable to draw attention to these post-mortem alterations in length in order to emphasize the necessity for measuring tagged sharks as soon as possible after recapture.

VII. DISCUSSION

It is evident that the school shark fishery is dependent on a slowly maturing homogeneous stock of low reproductive potential. Therefore, if this ability to reproduce was so lowered that the fishery no longer received sufficient recruitment to offset natural mortality and fishing rate we should have overfishing which, if continued, leads to depletion (Van Oosten 1946). In such a fishery as that of the school shark where the sexes mature slowly, it is essential for the future of the industry that the sharks are protected during the most vulnerable stage of their life cycle. Also because of the low fecundity of this species the juvenile mortality from fishing operations should be reduced to a minimum.

TABLE 11

POST-MORTEM ALTERATIONS IN LENGTH

Date	Sex	Living Length (mm)	Dead Length (mm)	Length Differences (mm)
26.viii.50	M	635	635	0
	F	685	677	−8
27.viii.50	M	470	456	−16
	F	482	486	+4
	F	612	611	−1
	M	651	647	−4
	F	602	610	+8
	F	683	693	+10
	F	438	443	+5
16.xii.50	M	535	514	−21
	M	553	525	−28

At present the pregnant females making their way to the inshore "pupping" areas are caught before they have released their young. Although many commercial fishermen release the unborn young hoping that they will survive, because those of a litter so released swim actively away, it is most unlikely that even a small proportion of the many thousands born this way do survive. Generally the yolk sac is protruding and the umbilical slit is still unclosed.

TABLE 12

PROGRESSIVE CHANGES IN LENGTH AFTER DEATH

Date	Time (hr)	Male Length (mm)	Female Length (mm)	Male Length (mm)	Female Length (mm)
26.ix.50	1100	500 (rigid)	445 (rigid)	660 (rigid)	
	1745	501 (limp)	445 (limp)	651 (rigid)	
27.ix.50	0930	492 (limp)	444 (limp)	648 (limp)	
26.viii.50	1200	635 (alive)	685 (alive)		
	1500	638 (dead)	691 (dead)		
27.viii.50	0900	631 (rigid)	677 (rigid)	460 (rigid)*	435 (rigid)*
28.viii.50	1230	635 (limp)	677 (limp)	465 (limp)*	442 (limp)*

* *Emissola antarctica* (Günther).

The mortality rate of full-term embryos with closed umbilical slits and without external yolk sacs, born prematurely, is approx. 75 per cent.

in 24 hr. This estimate was obtained from counts of dead prematurely born embryos lying in shallow water released the day before from females caught nearby in 3 fm. At the time of their removal from the mother, the embryos swam about actively. There was no mortality among the small sharks of the same size which had been handlined, tagged, and released in the same area. Therefore on the basis of this observation it is believed that most young sharks, born prematurely under less favourable conditions at sea, do not survive.

The destruction of juveniles in bays and estuaries by amateur and commercial fishermen is probably a big factor in the juvenile mortality of the school shark, which appears to have very few predators. These fishermen have a mistaken belief that all sharks are vermin and so great is their dislike and prejudice that all small sharks, whether of economic importance or otherwise, must be destroyed. Nearly all this unnecessary destruction could be prevented by suitable educational methods demonstrating the value of the juvenile sharks to the commercial fishery.

Since it has been determined that only approximately half the adult females bear young each year, the average number in a litter being 28 "pups", and that more males than females (54 : 46) are produced at birth but within 2 yr this ratio is reversed, presumably from higher male mortality, it follows that the most effective biological measures for the benefit of the fishery are provision of protection for the two most vulnerable stages in the life cycle of the school shark, namely, the 2-month period prior to birth and the subsequent 3-4 yr of their inshore life. These could be effected by prohibiting fishing for females during their inshore movement, by placing a minimum legal length restriction on the taking of juveniles, and by declaring known "pupping" areas as sanctuaries for the young sharks.

A forceful propaganda campaign could be undertaken to remove many of the prejudices against sharks and the unnecessary destruction of juveniles by fishermen.

VIII. ACKNOWLEDGMENTS

The author wishes to record his appreciation of the assistance received from the many representatives of the shark-fishing industry and particularly from the following professional fishermen: Mr. T. A. Wilson (Portarlington), Mr. E. C. Clark (Lewisham), Mr. B. J. Griffiths (Port Sorell), and Mr. E. E. Andrews (St. Helens).

Valuable help with the field studies was given by members of the staff of the Division of Fisheries, C.S.I.R.O., Mr. P. E. Gartner, Mr. W. Fletcher, Mr. J. C. Dowsett, Mr. W. A. Turner, Captain R. Downie, Master of the Division's research vessel, and Mr. D. E. Kurth, Research Zoologist, University of Tasmania, and Mr. B. C. Clennett, formerly of this Division. Mr. A. Proctor and Mr. R. Breach were responsible for the preparation of the figures used in the text.

The late Messrs. G. and T. Soderlund of Port Franklin, who were lost at sea in a storm, were particularly helpful by recording an extensive series of length measurements of their commercial shark catches made over 2 yr. Mr. V. McLaren and Mr. H. McGuiness, of Bridport, and Mr. B. T. Cuthbertson, Jr., of Hobart, also made supplementary measurements; Mr. W. P. Holman lent for study his records of the purchasing, handling, and marketing of shark.

Mr. A. D. Butcher, Director, and Mr. D. D. Lynch, Biologist, of the Victorian Fisheries and Game Department, made official records available and collected data on the Victorian shark fishery; the officers of the Fisheries Division of the Tasmanian Department of Agriculture also assisted with the study of the fishery in their State.

Mr. K. Morris, Section of Mathematical Statistics, C.S.I.R.O., Adelaide, was responsible for the statistical analysis of the collected data, and the author is grateful for this assistance.

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APPENDIX I

MOVEMENTS OF TAGGED SHARKS FROM INSHORE CENTRES

Tag No.	Length at Release (mm)	Date Released	Date Recaptured	Locality of Recapture	Duration of Freedom (wk)
Pittwater, Tas.					
*A*5281	1600	15.xii.49	13.vi.51	Kangaroo Head, Kangaroo I. (S.A.)	77.8
*B*5308	565	10.i.50	12.vii.52	20 Miles NE. of King I. (Tas.)	130.4
*B*5304	535	10.i.50	5.iii.53	10 Miles NE. of Ninth I. (Tas.)	164.4
*B*6076	350	13.iii.50	24.i.51	Eaglehawk Neck (inside) (Tas.)	45.3
*B*6955	865	8.xi.50	31.xii.52	35-40 Miles NW. of Bridport (Tas.)	154.8
*B*7563	450	10.i.51	23.ii.52	Opossum Bay, Pt. Arthur (Tas.)	58.3
*B*7567	585	10.i.51	8.vii.52	Lipson Reef, Kangaroo I. (S.A.)	77.7
Port Sorell, Tas.					
*A*1262	411	8.xii.48	7.i.49	Tamar Heads (Tas.)	4.3
*B*6724	448	29.iii.50	9.ix.51	Haystack Rock, Eden (N.S.W.)	75.4
*B*6726	538	29.iii.50	13.xii.51	20 Miles N. of Deal I. (Tas.)	89.3
St. Helens, Tas.					
*B*6871	625	27.vi.50	10.v.52	35 Miles SE. by ½E. of Lakes Entrance (Vic.)	97.1
Trial Bay, D'Entrecasteaux Channel, Tas. (1942 tagging programme)					
86	1470	2.vii.42	10.v.47	Recherche Bay (Tas.)	252.7
99	615	2.vii.42	21.x.47	Hogan Group (Vic.)	276
Portarlington, Vic.					
*A*58	589	15.iii.47	9.iv.50	Ninth I. (Tas.)	160.1
*B*5758	560	1.iii.50	13.v.52	Rivoli Bay (S.A.)	128.8
*B*5868	565	1.iii.50	1.xii.51	30 Miles W. of Stanley (Tas.)	91
*B*5892	600	1.iii.50	30.vii.52	Moonlight Head (Vic.)	126
*B*5921	610	2.iii.50	12.xii.51	50 Miles S. of E. of Kangaroo I. (S.A.)	92.8
*B*5969	560	2.iii.50	13.iii.53	12 Miles S. of Pyramid I. (Vic.)	158
*B*5975	760	2.iii.50	20.ii.52	42 Miles 12° W. of S. of Lakes Entrance (Vic.)	102.8
*B*6006	580	3.iii.50	19.vi.51	60 Miles S. of Port Phillip Heads (Vic.)	67.8
*B*6010	680	3.iii.50	29.xii.52	5 Miles NE. of Greenly I. (S.A.)	147.4
*B*7734	650	14.iii.51	1.x.52	30 Miles N. of E. of Hogan Group (Vic.)	80.8
*B*7745	632	14.iii.51	9.i.52	Portland (Vic.)	43
*B*7748	610	14.iii.51	30.iv.53	W. of Clark I. (Tas.)	111.1
*B*7809	665	14.iii.51	30.iv.53	Ninth I. (Tas.)	95.3
*B*7844	644	14.iii.51	19.xi.51	60 Miles S. of Port Phillip Heads (Vic.)	13
*B*7852	618	14.iii.51	1.x.52	30 Miles N. of E. of Hogan Group (Vic.)	80.8
*B*8006	445	15.iii.51	5.xii.51	Rhyll (Vic.)	38

APPENDIX II

NUMBER OF SHARKS TAGGED AND RECAPTURES FOR OFF-SHORE TAGGING POSITIONS, 1948-51

Location	1948	1949	1950	1951	Total
Tasmanian Waters					
St. Patrick's Head	—	—	8^{1}	—	8^{1}
Maria I. (70-130 fm)	—	16	18^{1}	—	34^{1}
Maria I. (45 fm)	—	6	1	—	7
Yellow Bluff (76-450 fm)	—	34	—	—	34
Yellow Bluff (35-60 fm)	—	3	—	—	3
Hippolyte Rock	—	4	—	—	4
Cape Pillar	—	4	—	—	4
Variety Bay, Bruny I.	1	1	—	—	2
Cape Connella, Bruny I.	—	2	—	—	2
South East Cape	—	3^{1}	—	—	3^{1}
New Harbour	—	1	—	—	1
Mewstone Rock	—	—	1	—	1
Port Davey	—	—	3	—	3
Cape Sorell (90-100 fm)	—	16	12	—	28
Black Pyramid (60 fm)	—	—	1	—	1
Black Pyramid (30-35 fm)	—	43^{2}	46^{1}	63	152^{3}
Hunter I. Passage	—	2	—	—	2
King I., East (15-20 fm)	2	—	—	14^{1}	16^{1}
King I., West (30-65 fm)	—	8	13	6	27
King I., West (80-110 fm)	—	69^{2}	66^{3}	1	136^{5} } 147^{5}
King I., West (130-400 fm)	—	—	5	6	11
Centre of Bass Strait	—	—	4^{2}	—	4^{2}
New South Wales waters					
Eden (66-90 fm)	—	18^{1}	—	—	18^{1}
Victorian waters					
Port Fairy (70-110 fm)	—	3	—	—	3
Port Fairy (280 fm)	—	3	—	—	3
Otway Bank	—	127^{3}	61^{4}	16	204^{7}
Pyramid Rock	—	14	—	—	14
Cliffy I.	1	—	—	—	1
Rame Head	3	8	—	—	11
Lakes Entrance (90 fm)	—	9	—	—	9
Tasmanian Waters — Furneaux Group					
Sisters and Craggy I.	—	22	—	—	22
Beagle Spit	9	24^{3}	21^{2}	—	54^{5}
Babel I.	19	1	—	—	20
Goose I.	—	30^{4}	34^{2}	5	69^{6}
Cape Barren I. (East 30-54 fm)	34	7	3	3	47
Cape Barren I. (East 84-230 fm)	—	4^{1}	17^{1}	15^{1}	36^{3}
Waterhouse I.	4	—	—	—	4
Banks Strait (55-60 fm)	—	—	18	—	18
East Banks Strait (70-100 fm)	—	—	—	70^{3}	70^{3}
West Banks Strait (18 fm)	—	—	—	1	1
Total	73	482^{17}	332^{17}	200^{5}	1087^{39}

APPENDIX III
RECAPTURES FROM OFF-SHORE TAGGING POSITIONS

Tag No.	Date of Release	Date of Recapture	Locality	Duration of Freedom (wk)
Otway Bank				
313	13.ix.49	19.vi.51	Lacepede Bay (S.A.)	92
*B*6107	14.iv.50	12.ii.51	12 Miles NW. Hunter I. (Tas.)	43.3
382	3.xii.49	8.iv.52	11 Miles SW. Cape Otway (Vic.)	122.4
151	14.iv.50	5.iv.52	5 Miles S. Port Campbell (Vic.)	103.1
383	19.xi.50	12.iv.53	27 Miles E. of King I.	125.3
*A*1845	27.ii.49	10.iii.53	29 Miles SSW. Apollo Bay (Vic.)	210.4
152	14.iv.50	2.ii.53	7 Miles SW. Night I. (Tas.)	146.4
Black Pyramid (30-35 fm)				
206	6.vi.49	20.iv.50	Streaky Bay (S.A.)	45.4
221	17.iv.50	13.ii.52	Albatross Rock (Tas.)	95.3
236	6.vi.49	1.v.52	Black Pyramid (Tas.)	151.4
King I. (Edge of shelf, 80-110 fm)				
275	9.vi.49	26.iii.50	Cape Otway (Vic.)	41.4
*B*6134	15.iv.50	14.xi.50	Port McDonnell (S.A.)	30.4
356	21.x.50	13.xii.51	6 Miles NE. Hunter I. (Tas.)	59.3
358	21.x.50	15.vi.52	15 Miles N. King I.	86.1
260	10.vi.49	20.iv.53	SE. of Sth. Neptune I. (S.A.)	201.4
King I. (East Side)				
506	2.iv.51	5.ix.52	Ulladulla (N.S.W.)	74.5
Centre of Bass Strait				
233	28.iv.50	24.viii.50	40 Miles S. Lakes Entrance (Vic.)	17
235	28.iv.50	1.xii.50	North Sisters I. (Tas.)	31
Beagle Spit (Flinders I.)				
*A*1717	27.i.49	4.iii.49	E. of Kent Group (Tas.)	5.1
*A*1719	27.i.49	13.v.49	10 Miles E. of Outer Sister I. (Tas.)	15.1
*A*1708	27.i.49	16.viii.49	14 Miles NE. Sisters Is. (Tas.)	28.7
252	30.iv.50	5.v.51	Discovery Bay (S.A.)	38.5
250	30.iv.50	23.xi.52	25 Miles NW. Kent Group (Tas.)	131
Goose I.				
*A*1996	2.x.49	6.ix.51	NNE. King I.	81.5
453	13.xii.50	25.ix.52	Bermagui (N.S.W.)	93.1
107	13.xii.49	28.iii.53	35 Miles W. of Robe (S.A.)	171.5
108	13.xii.49	3.xii.52	Rodondo I. (Vic.)	155.1
337	2.x.49	28.xi.52	10 Miles N. Waterhouse I. (Tas.)	164
328	13.x.50	12.ii.53	King I.	122.1
East Banks Strait				
599	18.iv.51	2.vii.52	Kiama (N.S.W.)	63
483	3.iii.51	29.i.53	20 miles NE. Outer Sister I. (Tas.)	99.7
474	3.iii.51	1.iii.53	Eddystone Pt. (Tas.)	104.1

Appendix III (*Continued*)

Tag No.	Date of Release	Date of Recapture	Locality	Duration of Freedom (wk)
Cape Barren I. (East, 84-230 fm)				
*A*2245	15.xii.49	3.iv.52	15 Miles E. Maria I. (Tas.)	120
322	9.x.50	3.iii.53	12 Miles E. Cape Lodi (Tas.)	120.7
652	17.vii.51	9.i.53	10 Miles NW. Waterhouse I. (Tas.)	77.4
Maria I. (70-130 fm)				
*B*6251	11.viii.50	18.vii.51	11 Miles ENE. Wineglass Bay (Tas.)	48.9
St. Patrick's Head				
428	12.xii.50	9.iii.53	6 Miles NE. Seymour Pt. (Tas.)	117
South East Cape				
162	22.v.49	13.v.51	South Cape (Tas.)	103
Eden				
362	15.x.49	21.i.53	20 Miles NE. Outer Sister I. (Tas.)	170.6

Appendix IV

LENGTH FREQUENCIES OF SHARKS CAUGHT BY RESEARCH VESSEL, 1948-52

Total Length (cm)	Western Bass Strait	Eastern Bass Strait	Total Length (cm)	Western Bass Strait	Eastern Bass Strait
60		2	116	1	—
1		2	7	2	2
2		1	8	3	2
3		2	9	7	1
4		2	120	5	1
5		—	1	5	1
6		—	2	12	—
7		—	3	6	4
8		1	4	6	2
9		—	5	14	3
70		2	6	6	2
1		—	7	5	3
2		—	8	4	3
3		1	9	9	2
4		1	130	21	7
5		3	1	8	2
6		1	2	11	5
7		2	3	14	7
8		1	4	11	3
9		2	5	23	7
80		1	6	19	6
1		1	7	30	10
2		2	8	18	7

APPENDIX IV (*Continued*)

Total Length (cm)	Western Bass Strait	Eastern Bass Strait	Total Length (cm)	Western Bass Strait	Eastern Bass Strait
3		1	9	31	6
4		2	140	38	20
5		1	1	32	8
6		2	2	30	16
7		2	3	33	17
8		—	4	27	10
9		—	5	54	34
90		2	6	37	13
1		3	7	31	13
2	1	3	8	24	16
3	—	1	9	24	18
4	1	—	150	48	38
5	—	1	1	27	18
6	—	2	2	23	15
7	1	5	3	23	11
8	—	2	4	19	13
9	1	2	5	14	10
100	1	2	6	8	5
1	1	4	7	14	2
2	—	2	8	8	4
3	1	1	9	3	2
4	—	5	160	12	5
5	—	3	1	—	—
6	2	4	2	2	1
7	3	—	3	3	1
8	2	1	4	2	2
9	—	2	5	—	—
110	1	5	6	—	—
1	1	1	7	—	—
2	1	3	8	—	1
3	3	1	9	—	—
4	3	2	170	1	—
5	4	—			
				835	471

POPULATIONS OF BARRACOUTA, *THYRSITES ATUN* (EUPHRASEN), IN AUSTRALIAN WATERS

By M. BLACKBURN* and P. E. GARTNER*

(*Manuscript received March* 9, 1954)

Summary

Different populations of barracouta (Scombriformes: Acinaceidae), the principal Australian fish of commerce, have been recognized by a study of differences in the following: spawning season; size composition of adult stock; and seasonal movements and annual fluctuations as revealed by records of catch and fishing effort. Tagging experiments gave little information because of the low rate of commercial exploitation of the populations.

There are probably five populations in southern coastal waters, which make migrations to certain areas as follows: one in winter and spring to eastern Victoria and southern New South Wales, one from spring to autumn to Bass Strait and its western approaches, one in summer and autumn to eastern Tasmania, one in autumn and winter to South Australia and western Victoria, and one (possibly not distinct from the previous population) in autumn and winter to the south coast of Western Australia. Spawning and feeding take place in the course of these migrations. Little is known about the populations when they are not migrating, but the three first-mentioned groups all appear to seek the neighbourhood of eastern Bass Strait between the migratory seasons. The fish prefer waters of about 13-18°C and tend to vacate areas when they become cooler or warmer than this.

Only the Bass Strait and eastern Tasmanian populations are significantly fished and the size of the catches is generally governed by the demand. However, there have been occasional years of scarcity, such as 1950-51 and 1951-52 in Bass Strait and 1951-52 in eastern Tasmania. These represent natural fluctuations (there is no evidence of depletion of any population) and for the Bass Strait population they are probably fluctuations in availability in the fishing areas rather than in abundance of the whole population. It is considered that the combined Australian populations could yield 10 times as much as the present annual catch of 6,000,000 lb (beheaded and cleaned) when fluctuations were not adverse.

I. INTRODUCTION

The barracouta, *Thyrsites atun* (Euphrasen), is a scombriform fish of the family hitherto called Gempylidae. According to Whitley (1951) the type of *Gempylus* Cuvier 1829 is conspecific with the type of *Acinacea* Bory de St. Vincent 1804 and the names *Acinacea* and Acinaceidae must replace *Gempylus* and Gempylidae.

Whitley (1951) also stated that the genus *Thyrsites* was established by Lesson in 1831 with *T. lepidopodea* Cuvier MS. as type, not by Cuvier 1829 with *Scomber atun* Euphrasen as type, as stated by Jordan and Evermann (1917). He thought *atun* should be placed in a separate genus for which the name *Leionura* Bleeker 1860, with *L. esox* Bleeker = *Thyrsites atun* as type, is available. This would be permissible but so would

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* Division of Fisheries, C.S.I.R.O., Cronulla, N.S.W.

the retention of *atun* in the genus *Thyrsites,* as the differences between *atun* and *lepidopodea* (*lepidopoidea, lepidopoides* of authors) are not great (Forest and Legendre 1950). The present authors therefore retain the familiar combination *Thyrsites atun* on the grounds of convenience.

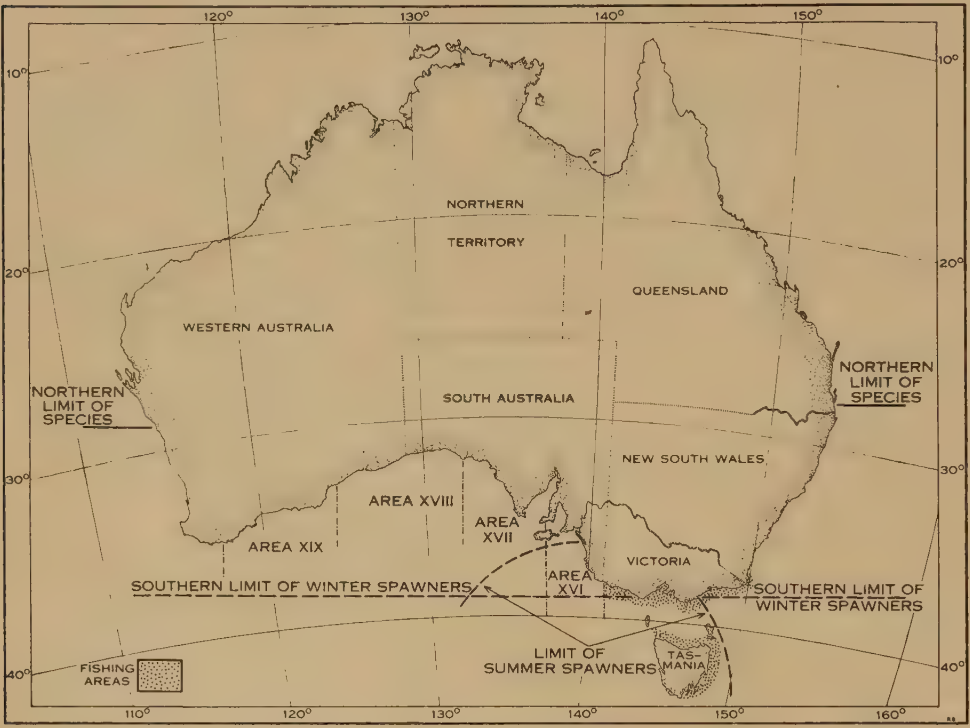
120°
130°
140°
150°
10°
20°
30°
40°
110°
160°
NORTHERN
TERRITORY
QUEENSLAND
WESTERN AUSTRALIA
SOUTH AUSTRALIA
NEW SOUTH WALES
VICTORIA
NORTHERN LIMIT OF SPECIES
NORTHERN LIMIT OF SPECIES
AREA XVIII
AREA XVII
AREA XIX
AREA XVI
SOUTHERN LIMIT OF WINTER SPAWNERS
SOUTHERN LIMIT OF WINTER SPAWNERS
LIMIT OF SUMMER SPAWNERS
TAS-MANIA
FISHING AREAS

Fig. 1.—Australia, showing the range of the barracouta, of winter and summer spawners, and of the fishery.

A long list of literature on *T. atun* is given by Whitley (1931). Norman (1937) regarded the South American *Thyrsites chiliensis* Cuvier and Valenciennes as conspecific although Whitley did not. The occurrence of *T. atun* in Western Australia is recorded by Whitley (1948). The species, as at present known, occurs in the coastal waters of southern Africa (type locality), southern Australia, southern South America, the Falkland Is., New Zealand, and the islands of Tristan da Cunha and St. Paul.

In Australia the barracouta occurs in neritic waters south of Moreton Bay on the east coast and Houtman's Abrolhos (where one specimen was recently taken) on the west coast (Fig. 1, northern limits). But its occurrence as a common species is virtually confined to the south coast of the continent and Tasmania (Blackburn 1950, and this paper) and the area of the commercial fishery is even more restricted (Fig. 1).

Table 1 shows the recorded barracouta catches of each of the three Australian States in which there is a fishery, in each year for which the information is available. This table has been revised and brought up to date from Table 2 of Blackburn (1950), who indicated the sources of the

TABLE 1

RECORDED CATCHES OF CLEANED HEADLESS BARRACOUTA IN AUSTRALIA (LB)

Year	Victoria	Tasmania	New South Wales	All States
1911	2,377,685			
1912	2,656,351			
1913	2,748,671			
1914	2,485,877			
1915	2,845,558			
1916	3,738,277			
1917	2,532,566			
1918	3,115,365			
1919	2,965,486			
1920	3,549,498			
1921	3,974,757			
1922	2,901,230			
1923	1,879,189	2,947,012		4,826,201
1924	2,450,904			
1925	2,954,483			
1926	2,117,567			
1927	3,270,934			
1928	2,544,877			
1929	1,779,027	2,977,361		4,756,388
1930	4,217,609			
1931	5,056,510	1,360,250		6,416,760
1932	4,047,050	903,617		4,950,667
1933	4,461,435			
1934	4,517,869	1,693,670		6,211,539
1935	4,138,408	1,413,943		5,552,351
1936	4,073,884	1,498,892		5,572,866
1937	5,281,305	1,637,377		6,918,682
1938	5,487,941	1,888,357		7,376,298
1939	3,673,787	702,655		4,376,442
1940	2,439,852	277,769		2,717,621
1941	2,611,064			
1941-42	2,515,660	1,798,041		4,313,701
1942-43	2,873,809	2,444,911		5,318,720
1943-44	3,745,410	3,084,414	505,303	7,335,127
1944-45	3,558,215	5,803,932	881,281	10,243,428
1945-46	7,347,308	6,116,652	609,130	14,073,090
1946-47	5,856,134	4,568,070	118,712	10,542,916
1947-48	5,522,357	7,070,308	70,927	12,663,592
1948-49	5,541,472	8,032,459	91,508	13,665,439
1949-50	4,627,342	4,411,255	9,396	9,047,993
1950-51	3,221,572	3,221,510	20,896	6,463,978
1951-52	3,673,765	2,487,063	76,566	6,237,394

catch records. Except for Tasmanian figures before 1941-42, all figures were totalled by the authors from monthly totals compiled by the Fisheries Departments of the States. The figures are for weight of fish with head and viscera removed, which is normally about 70 per cent. of weight in the round. The Australian catch of barracouta on the basis of estimated round weight is usually as high as or higher than the Australian catch of any other aquatic species (except whales) on a similar basis. This was so even in 1951-52 when the barracouta catch was lower than in any of the preceding 8 years; on a round weight basis this catch was equal to or a little greater than that of sea mullet, *Mugil cephalus* Linnaeus, the next most important species.

In spite of the commercial importance of the barracouta in Australia, in South Africa where annual catches are apparently larger (Skaife 1949), and elsewhere, very little work on the biology of the species has been reported (see Section VI). The present paper deals mainly with the recognition of different populations of barracouta in Australian waters and some characteristics of the populations. Most of the data were obtained in a special investigation which began in 1948, but use has been made of some earlier observations.

In fisheries biology the recognition of different populations within a species is generally the result of observations on geographical variation in morphological characters, or tagging experiments, or both. The work reported here is not, in the main, of either kind. It is more the outcome of observations on geographical variation in ecological characters, mainly seasonal and annual changes in the behaviour and composition of groups of fish. In this it resembles the work of Sette (1950) who distinguished two populations of mackerel (*Scomber scombrus* Linnaeus) in the western North Atlantic by observations on size composition of catches together with the time sequence of catches at various points along the coast. He said: "This evidence, although indirect, has a notable advantage over the more direct method of tagging. It enables one to deal with a much larger portion of the population and to obtain a much more definite estimate of the relative numbers of individuals involved in the movements (i.e. distinguish mass movements from stragglings) than can be gained from the relatively small numbers usually tagged. Nevertheless, tagging experiments were done, which furnish confirmation." In the barracouta investigation the tagging experiments unfortunately furnish very little relevant information; on the other hand there is additional indirect evidence, principally relating to seasons of spawning, of the existence of different populations.

Little attention was given to the possibility of distinguishing barracouta populations by work on morphological characters, a method which has not proved very successful in scombriform species. It was felt at the beginning that much time might be spent on making counts and measurements, of which most would probably prove to be useless for distinguishing populations and none would probably be useful for any other purpose, on only a few thousand fish. Subsequent experience showed that time would not have been available to deal with samples in this way under the conditions in which most of the fish were of necessity handled.

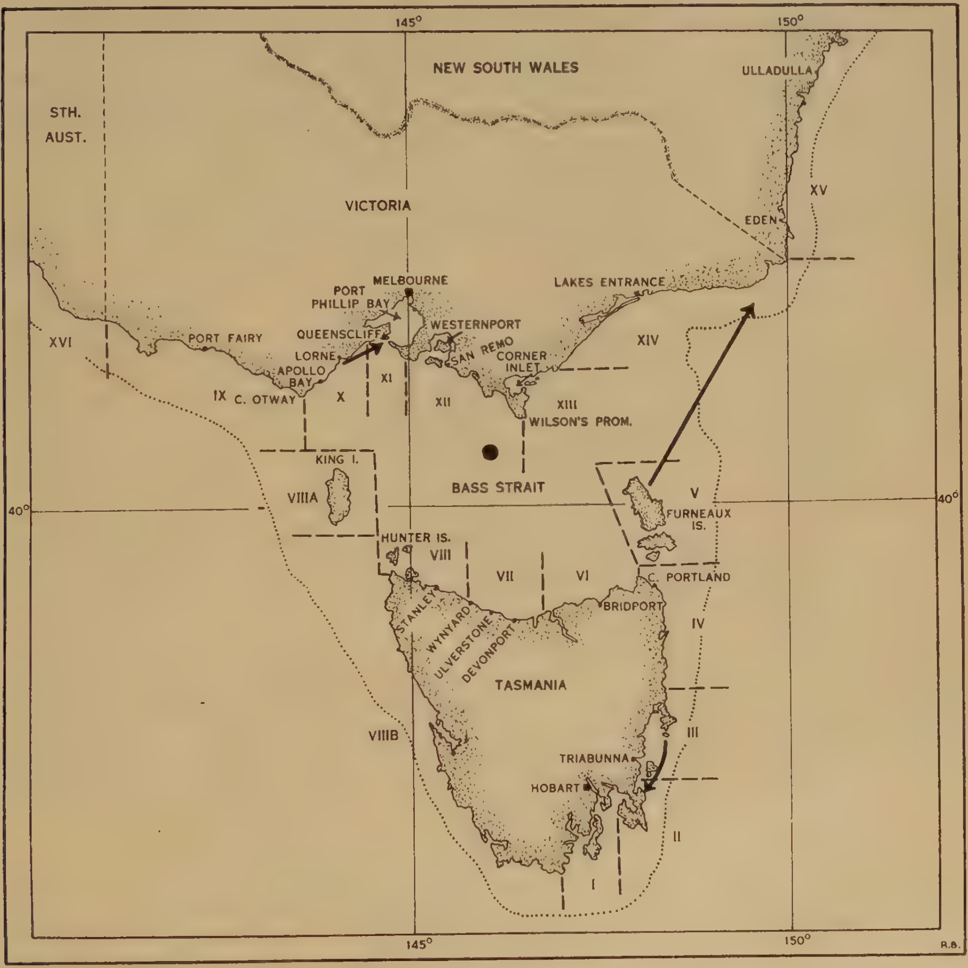
145°
150°
NEW SOUTH WALES
ULLADULLA
STH. AUST.
VICTORIA
XV
EDEN
MELBOURNE
PORT PHILLIP BAY
LAKES ENTRANCE
WESTERNPORT
XVI
PORT FAIRY
QUEENSCLIFF
LORNE
APOLLO BAY
SAN REMO
CORNER INLET
XIV
XI
IX
C. OTWAY
X
XII
XIII
WILSON'S PROM.
KING I.
BASS STRAIT
VIIIA
V
40°
40°
FURNEAUX IS.
HUNTER IS.
VIII
VII
VI
C. PORTLAND
BRIDPORT
STANLEY
WYNYARD
ULVERSTONE
DEVONPORT
IV
TASMANIA
III
VIIIB
TRIABUNNA
HOBART
II
I
145°
150°
R.B.

Fig. 2.—South-eastern Australia, showing numbered areas referred to in the text (see Fig. 1. for other areas). The heavy arrows indicate apparent movements of recaptured tagged fish; the black circle indicates the furthest off-shore recorded occurrence of barracouta in the central basin of Bass Strait; and the dotted line represents the edge of the continental shelf.

Most of the data of this paper are grouped according to areas. Twenty-one areas are recognized; they are described below and shown in Figures 1 and 2. Areas I to VIII have been recognized for some years by the Tasmanian State fisheries authority for the purpose of grouping records of fish catch and effort and it was therefore convenient to use them for the present study, although it was thought desirable to divide the large area VIII into VIII, VIII*A*, and VIII*B*. The Victorian coast was divided into six areas (IX to XIV) comparable in size with the Tasmanian areas, largely on the basis of important geographical features and on the ranges of the barracouta fishing fleets of the different ports; and the rest of the coast was rather arbitrarily divided into five much larger areas (XV to XIX). It was necessary to recognize so large a number of small areas in Tasmania and Victoria, rather than a small number of large ones, to avoid concealing the evidence of coastwise migration which is presented in Section V(*a*) and to minimize the risk of grouping data of different populations under the same area heading. However, for the convenience of the reader some adjacent areas have been grouped for the purpose of presenting data on spawning and feeding seasons (Section III, Figs. 3-5).

	Tasmania
Area I	South East Cape to Pittwater
Area II	Pittwater to Cape Bernier
Area III	Cape Bernier to Cape Lodi
Area IV	Cape Lodi to Cape Portland
Area V	Furneaux Is.
Area VI	Cape Portland to Badger Head
Area VII	Badger Head to Table Cape (includes Wynyard)
Area VIII	Table Cape to Cape Grim
Area VIII*A*	King I.
Area VIII*B*	Cape Grim to South East Cape
	Victoria
Area IX	South Australian border to Cape Otway
Area X	Cape Otway to Split Point
Area XI	Split Point to Cape Schanck (includes Port Phillip Bay)
Area XII	Cape Schanck to Wilson's Promontory
Area XIII	Wilson's Promontory to Shallow Inlet
Area XIV	Shallow Inlet to New South Wales border
	New South Wales
Area XV	New South Wales, all waters; but especially within 100 miles of the Victorian border, where the species is most common.
	South Australia and Western Australia
Area XVI	Victorian border to long. 137° 30′ E.
Area XVII	Long. 137° 30′E. to Cape Adieu
Area XVIII	Cape Adieu to Point Culver
Area XIX	Point Culver to Albany

Measurements of barracouta reported in this paper are all to the nearest cm and refer, unless otherwise stated, to length from tip of lower jaw (the most anterior part of the fish) to the fork of the caudal fin ("length to caudal fork" or "L.C.F."). The measurements in Section IV were made on beheaded fish (commercial fishermen behead and clean their barracouta as soon as possible after capture) by measuring from the most anterior part of the carcase to the caudal fin fork ("cleaned length") to the nearest cm. In length frequency polygons these measurements have been plotted according to cm of cleaned length (see lower legend on the length axis in Figs. 6-9) but points on the curves can be identified in terms of L.C.F. by reference to the upper legend on the length axis. This legend was obtained from an equation,

$$\text{Length to caudal fork} = (1.165 \times \text{cleaned length}) + 5.329,$$

which was calculated from 5363 pairs of measurements of Victorian and Tasmanian barracouta.

Slight errors in using this equation could result from the fact that the data on which it is based were obtained by beheading all the fish in the manner of fishermen in Areas VIII and XIV, although other methods of cutting are used in other areas. But a survey of cutting methods in all the main ports showed that the difference in cleaned length, due to different methods of cutting, would not be greater than about 0.5 cm in small fish or 1.0 cm in large ones, and for the purposes of this paper such differences are unimportant.

A convenient approximate statement of the relationship of cleaned length to L.C.F. is that the former is slightly more than three-quarters of the latter.

Nearly all the barracouta which are captured are taken by trolling or pole-fishing at or near the surface of the sea (Blackburn 1950). The account which follows is primarily one of surface manifestations of barracouta populations. The probable extent and nature of subsurface occurrences are discussed in Section VI.

II. TAGGING EXPERIMENTS

The first barracouta tagging in Australian waters was done in November 1948. Up to the present (October 1953) 4598 fish have been tagged and released.

The adult barracouta is large, active, and ferocious, and its scales are highly deciduous. Great care had to be taken in unhooking, tagging, and releasing the fish to ensure that neither they nor the operators suffered any material injury. Until May 1951 each fish was measured before release, which added to the time and complexity of the operation; but even so each fish was only out of water for about 1 min. Only one tag was attached to each fish but seven types of tags were employed during the 5 yr of tagging, two of them on two different parts of the body. There were thus nine different tagging procedures in all; the numbers used in each procedure and the regions of liberation are shown in Table 2.

The types of tags used, described below, are named in accordance with Rounsefell and Everhart (1953).

White Petersen tags (see Olsen 1953 for specifications) were attached to the dorsal part of the caudal peduncle.

Grey Petersen tags, in other respects the same as the white Petersens, were attached to the caudal peduncle and later to the flesh of the back of the fish just anterior to the second dorsal fin. These replaced the white tags because it was thought that the white tag, being more conspicuous, might render the tagged fish vulnerable to attack by natural enemies.

Body cavity tags (the smaller size described by Olsen 1953) were inserted through a vertical cut in the flank between the mid-ventral line and the normal position of the tip of the pectoral fin, and pushed forward.

Strap tags of monel metal (the "smaller" type mentioned by Rounsefell and Everhart 1953) were used on the operculum and in front of the second dorsal fin.

Collar tags (plastic spiral, poultry leg-band type) were placed around the caudal peduncle.

Hydrostatic tags, each 48 mm long, were placed in front of the second dorsal fin, on loops of stainless steel wire.

Safety pin tags, of silver, each about 20 mm long when closed, were attached before the second dorsal fin.

Considerable publicity was given to this tagging and rewards were offered for returned tags. But only seven tags, 0.15 per cent. of the total number released, have so far been returned.

The only returns were of Petersen tags (Table 2). Of the 1145 white Petersens used on the caudal peduncle two (0.17 per cent.) were returned, but the 1144 grey Petersens used in the same way yielded four returns (0.34 per cent.). The 270 grey Petersens used on the back yielded one returned tag (0.37 per cent.):

Slightly higher percentages are obtained by comparing recaptures with groups of releases (same area, same month) from which recaptures were made. There were five such groups of releases, namely 79 white Petersens, 352 white Petersens, 93 grey Petersens (caudal peduncle), 465 grey Petersens (caudal peduncle), and 235 grey Petersens (back); the numbers returned were respectively one, one, one, three, and one (these are discussed below as first tag, second, third, etc.), the percentages being 1.27, 0.28, 1.08, 0.65, and 0.43.

The first tag was used in area X on November 28, 1948, and the fish was recaptured in area XI on December 13, 1948. It had moved at least 35 miles in 15 days (see Fig. 2). The second was used in area V on April 2, 1949 and the fish was recaptured in a commercial trawl in area XIV about August 18, 1949. It had moved at least 120 miles in about 135 days (Fig. 2); this was the greatest movement recorded. The third tag was put out in area XI on October 8, 1949, and recovered in the same

TABLE 2

SUMMARY OF BARRACOUTA TAG RELEASES (NUMBERS OF RECAPTURES IN BRACKETS)

Region of Release	White Petersen	Grey Petersen		Body Cavity	Strap		Collar	Hydro-static	Safety Pin	Total
		Tail	Back		Oper-culum	Back				
Areas I-IV (eastern Tasmania)	167	411	245(1)	161	62		136		76	1258(1)
Area V (Furneaux Is.)	359(1)	10		49	50	1				469(1)
Areas VI-VIII (northern Tasmania)	134			13	49	34				230
Area VIIIA (King I.)	283	13	25		30			1		352
Areas IX-XIII (southern Victoria)	183(1)	710(4)		1070	150	4		129	24	2270(5)
Area XIV (eastern Victoria)	6									6
Area XV (southern New South Wales)	13									13
Total	1145(2)	1144(4)	270(1)	1293	341	39	136	130	100	4598(7)

area on December 3, 1949. The fish might not have moved during its 56 days of freedom. The fourth, fifth, and sixth were all used in area XI on March 28, 1950, and recovered in the same area. The dates of recapture of two of the fish could not be ascertained, even approximately; the tags were returned to the laboratory on June 14 and August 1, 1950. The third fish was recaptured in the first days of December 1950; thus it was free for about 250 days (the longest period of freedom for any of the recaptured fish) and might not have moved during that time. The seventh was put out in area III on February 14, 1953 and the fish was retaken in area II on March 28, 1953. It had moved at least 40 miles in 42 days (Fig. 2).

In connection with the second recovery it is of interest that a frequency polygon of the lengths of 662 barracouta which were measured in area V in April 1949 was almost identical with a polygon of lengths of 688 fish which were measured in area XIV in August 1949. Both samples were taken at random.

This number of recaptures is much too small from which to draw conclusions about the number and location of possible barracouta populations. The most interesting feature of the tagging operations is the very low percentage of tags recovered; the highest recovery figure, for a batch of fish tagged in the same way in the same month in the same area, is only 1.27 per cent.

Possible explanations, full or partial, might be: (*a*) low rate of exploitation by the fisheries, (*b*) tagging in unfished areas or migration of fish to such areas, (*c*) shedding of tags, (*d*) mortality due to tagging, or (*e*) failure of finders to return tags.

Explanation (*b*) can reasonably be neglected; 821 of the total of 4598 tagged fish were released in unfished areas (areas V, VIII*A*), but one of them (the second recovery discussed above) was retaken in a fished area, and it is shown elsewhere (Section V(*a*)) that there is seasonal movement of barracouta between unfished and fished areas. It seems very probable that the great majority of the tagged fish, apart from any which lost their tags or died from being tagged, passed some of their subsequent life in a fishing area. Explanation (*e*), failure to return tags, can also be neglected; Australian fishermen have an interest in tagging experiments which was shown by the return of considerable numbers of tags from fish of other species at the same time and in the same area as that of the barracouta tagging experiments.

Tag shedding (*c*) and tagging mortality (*d*) probably did occur to some extent. Fishermen in a few areas in which barracouta tagging had been done reported the capture of a few fish which looked as if they had shed Petersen tags from the caudal peduncle. There is no direct evidence of tagging mortality, and the fishermen who returned the seven tags perceived no sign that the barracouta had been harmed. As indicated above, increased attention was given to the welfare of the tagged fish as the experiments proceeded, but there was no increase in the rate of recovery.

There are thus no reasons to suppose that losses of tags from any cause were particularly great. On the other hand the remaining explanation (*a*) of the low percentage of tags recovered, i.e. low rate of exploitation by the fisheries, is highly credible; to quote Blackburn (1950), "At the stage at which it is commercially useful, the barracouta is an open-sea fish, but . . . it is sought only by vessels which operate very close to their home ports, for the most part carrying no ice, and using gear which permits considerable escape. Most of this is again a function of the limited demand." If losses of tags from all causes were to be estimated at the very high figure of 90 per cent. and the number of recovered tags expressed only as a percentage of the 10 per cent. remainder, these percentages would still be low. For white Petersen tags they would range from 2 per cent. (for the total of 1145 tags) to 12.5 per cent. (for the 79 tags used in area X in November 1948) ; for grey Petersens on the caudal peduncle they would range from 3.5 per cent. (for the total of 1144 tags) to 11 per cent. (for the 93 tags used in area XI in October 1949).

This species has also been tagged in South African waters, with a strap tag on the caudal peduncle (Von Bonde 1928). The numbers released and recaptured have been of a similar order to those in Australian waters (Marchand, personal communication). One fish was tagged near Walvis Bay (south-west Africa) on November 16, 1934 and recaptured in False Bay, near the Cape of Good Hope, on March 19, 1937, having travelled at least 880 miles during its 2 yr 4 months of freedom.

III. SPAWNING AND FEEDING SEASONS

(*a*) *Length at First Maturity*

The stages in maturity undergone by barracouta gonads, both male and female, are described below. It is possible to distinguish between the ovary stages up to and past spawning and the testis stages are almost as clearly defined. These stages were generally distinguished macroscopically in the field but some ovaries were examined microscopically.

The four types of ova noted by Fairbridge (1951) can be recognized in barracouta ovaries. Their main features are as follows:

Type (*a*).—Small polygonal or oval ova, transparent, with nucleus visible (0.05-0.15 mm diameter).

Type (*b*).—Nearly round, almost opaque due to increase of yolk granules, but nucleus visible (0.15-0.3 mm).

Type (*c*).—Large, round, opaque ova, nucleus obscured (0.3-0.6 mm).

Type (*d*).—Ripe ova, transparent, with nucleus and oil droplet visible, large and round (0.6-0.75 mm).

Female gonad stages

Stage 1.—Ovary of a fish which is virgin, i.e. has never shed ova. A pinkish strap, less than three-quarters of the length of the body cavity, with a rounded edge. Ova are generally type (*a*) but some larger fish of this stage may have some early type (*b*) ova.

Stage 2.—This occurs in two kinds of fish. In developing virgins the ovary is pink and glassy, and at least three-quarters of the length of the body cavity. In recovering spent fish it is usually as long as the body cavity and may be flabby and bloodshot at the extreme posterior end. Individual ova are not discernible macroscopically; in virgins most ova are type (*a*) but about 5 per cent. are early type (*b*) ova. Recovering spent individuals may have up to 10 per cent. type (*b*) ova and a few type (*c*) ova.

Stage 3.—Ovaries almost the length of the body cavity but not of maximum bulk, opaque and becoming yellowish. Ova not yet discrete as seen with the naked eye, about 70 per cent. type (*a*), 15-20 per cent. type (*b*), and 10-15 per cent. type (*c*) ova.

Stage 4.—Ovaries are full length of body cavity but still not swollen to full size, still opaque, yellowish pink. Ova discrete as seen with naked eye. About 60 per cent. of ova are type (*a*), 20 per cent. are type (*b*), and almost 20 per cent. are type (*c*).

Stage 5.—The ovary is the full length of the body cavity and swollen to completely fill the available space. Ovary and ova are becoming transparent. Ova are much larger than in stage 4, discrete, but not quite spherical; about 30 per cent. are type (*a*), 35 per cent. are type (*b*), 30 per cent. are type (*c*), and about 5 per cent. are type (*d*). The late stage 5 ovary shows a further great increase in type (*d*) ova and a drop in the percentage of type (*c*). Some type (*c*) ova are surrounded with a clear membrane (about 0.03 mm in thickness) which does not appear on the type (*d*) ova. Ova cannot be expressed from stage 5 female fish by pressure on the belly of the fish.

Stage 6.—All fish of this stage express ova under light stripping pressure on the belly. The ovary is pinkish, clear, and granular in appearance. Sometimes it is partly spent with the posterior portion flaccid and bloodshot. Ova are 20 per cent. type (*a*), 50 per cent. type (*b*) of maximum size, 10 per cent. type (*c*), and about 20 per cent. type (*d*), the last group constituting the bulk of the ovary. When shed these are almost 1 mm in diameter. This is the running ripe stage which has rarely been seen in female fish.

Stage 7.—No ova are expressed under light stripping. The ovary is generally bloodshot and flaccid, sometimes still partly swollen and transparent at the anterior end. About 75 per cent. of the residual ova are type (*a*), 20 per cent. are type (*b*) (these will develop into the next batch of ova to be spawned), and about 5 per cent. are type (*c*) ova undergoing breakdown, but these ova cannot be seen macroscopically. This stage is succeeded by stage 2.

Male gonad stages

Stage 1.—Juvenile, virgin stage, which is difficult to separate from the female, but the gonad is more ribbon-like than the stage 1 ovary and has a sharper edge; it is less than three-quarters of the length of the body cavity.

Stage 2.—In a virgin fish the testes are mottled creamy-red ribbons with a sharp edge, about three-quarters as long as the body cavity. In the recovering spent stage the broad reddish organ runs the full length of the body cavity.

Stage 3.—Testis larger and creamy pink in colour but in virgin fish not yet as long as the body cavity. The testes do not completely fill the body cavity and there are no swollen blood vessels. A more swollen stage than 2 but difficult to separate from 4.

Stage 4.—Testes full length of body cavity and almost completely filling it. No milt is expressed by slight pressure on the gonad.

Stage 5.—Testes are pinkish white, of maximum size, with the blood vessels on the gonad large and full. Milt can be expressed by light pressure on the gonad itself, but not by gentle pressure on the belly.

Stage 6.—Running ripe testes that extrude milt when gentle stripping pressure is applied to the belly of the fish.

Stage 7.—No milt is expressed with gentle pressure. The testes are broad, flaccid, and bloodshot, but more solid in substance than the sack-like stage 7 ovary of the female. This stage is succeeded by stage 2.

The scarcity of the female stage 6 may indicate that spawning takes place very quickly; it possibly occurs at a time of day when fish are not generally caught (see Section VI). But stage 6 males are very common.

Table 3 summarizes the sex and gonad stages of all barracouta for which these observations were made (data of all localities and years combined). Fish below 35 cm L.C.F., which rarely occur in the commercial catch, are often hard to sex. The rare female stage 6 has been included with stage 7, and the least length at stages 5 and 7 must be used to find the length of females at first maturity. One stage 5 female has been found among fish of 54 cm L.C.F. but this stage is more common among fish over 60 cm; similarly there are stage 7 females as small as 52 cm but they are more common among fish over 61 cm. Males appear to ripen at slightly smaller sizes: the smallest fish at stages 5, 6, and 7 measured 50, 51, and 48 cm respectively. Thus the smallest spawning barracouta are about 50 cm L.C.F. The largest fish noted with stage 1 gonads measured 81 cm. The percentage of fish with gonads more advanced than stage 1, i.e. those which were spawning, had spawned, or would probably have spawned in the same year, rises sharply in successive

TABLE 3

SEX AND GONAD STAGES OF BARRACOUTA OF STATED LENGTHS (L.C.F.); ALL AUSTRALIAN OBSERVATIONS TO END MAY 1953. ♀ STAGE 6 WAS RARE AND IS INCLUDED WITH ♀ STAGE 7

L.C.F. (cm)	Gonad Stages														All Stages				Total Beyond Stage 1 (%)			
	1			2		3		4		5		6	7									
	?	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♂	♀	?	♂	♀	Total	?	♂	♀	Total
13-35	66	14	11												66	14	11	91				
36	2	2	2		1	2									2	4	3	9		50	33	33
37	1	1		2		1	1								1	4	1	6		75	100	67
38	3	1	2		1		1								3	1	4	8			50	25
39	1					1									1	1		2		100		50
40	1	1	1	1											1	2	1	4		50		25
41																						
42		3	2													3	2	5				
43		1														1		1				
44		1														1		1				
45			1	1	3											1	4	5		100	75	80
46	1				1										1		1	2			100	50
47		3	2		2											3	4	7			50	29
48		6	3	1	3								1			8	6	14		25	50	31
49		4	2		2											4	4	8			50	25
50		8	9	1		1				1			1			12	9	21		33		20
51		3	5	3								1	2			9	5	14		67		43
52		9	8	2	4							1	2	3		14	15	29		36	47	41
53	1	7	1	3	8		1		1						1	10	11	22		30	88	59
54	1	25	12	4	10	1	4				1	3		2	1	33	29	63		26	58	40
55		26	14	4	11	1		1		1		3	1	2		37	27	64		30	48	38
56	1	18	16	7	18	3	3	2	1	2		5	4		1	41	38	80		55	57	56
57		20	9	10	22	2	7	1		1		3	6	2		43	40	83		53	78	65
58		21	17	16	23	4	3					10	4	6		55	49	104		61	64	62
59		19	17	13	37	7	3		4	1		12	5	6		57	67	124		67	75	70
60	1	23	10	21	50	5	4	3	2	4	2	11	8	7	1	75	75	151		68	85	78

TABLE 3 (*Continued*)

L.C.F. (cm)	Gonad Stages 1			2		3		4		5		6	7		All Stages				Total Beyond Stage 1 (%)			
	?	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♂	♀	?	♂	♀	Total	?	♂	♀	Total
61		22	13	18	48	3	10	3	4	6	3	9	15	11		76	89	165		70	84	78
62		19	10	24	40	8	10	5	4	2	3	23	10	14		91	81	172		79	89	86
63		11	4	20	38	3	15	1	6	7	4	19	19	14		80	81	161		86	96	91
64		5	5	17	43	5	17	4	8	14	7	32	23	19		100	99	199		95	95	95
65		6	4	19	29	3	22	3	8	13	4	28	21	21		93	88	181		95	93	94
66		8		21	55	7	16	7	13	13	10	36	28	37		120	131	251		93	100	97
67		12	1	23	58	5	8	1	9	11	9	34	18	28		104	113	217		88	99	92
68		11	3	25	50	5	25	6	10	15	10	36	39	39		137	137	274		92	98	94
69		5		18	66	3	25	5	3	6	7	33	30	23		100	124	224		95	100	99
70		4	1	22	62	6	17	2	3	15	8	43	40	35		132	126	258		93	99	96
71		3	1	17	43	2	16	4	15	9	9	35	39	27		109	111	220		98	99	98
72		1	2	17	49	2	21	5	7	13	8	44	31	37		113	124	237		99	98	98
73		4		9	39	7	24	3	8	15	9	37	34	40		109	120	229		97	100	98
74		2		18	50	2	18	4	15	8	8	43	35	34		112	125	237		98	100	99
75		2		14	32	6	5	6	18	6	9	41	33	27		108	91	199		98	100	99
76		4		17	42	4	23	3	9	11	14	37	46	36		122	124	246		97	100	98
77		2		13	56	5	18	6	14	12	8	33	32	27		103	123	226		98	100	99
78		4	1	22	66	5	14	6	11	12	19	39	41	40		129	151	280		97	100	98
79		3		22	55	7	21	2	14	7	17	39	38	43		118	150	268		98	100	99
80			1	26	61	8	16	4	15	9	19	45	45	54		137	166	303		100	100	100
81		1		18	52	4	15	4	12	15	8	47	34	49		123	136	259		99	100	100
82				30	74	6	20	8	13	14	18	55	44	69		157	194	351		100	100	100
83				33	77	10	24	9	12	8	16	79	42	64		181	193	374		100	100	100
84				34	74	9	28	8	27	14	33	58	55	71		178	233	411		100	100	100
85				24	72	7	29	10	26	15	38	79	35	63		170	228	398		100	100	100
86				17	63	9	26	4	23	16	25	66	43	60		155	197	352		100	100	100
87				23	65	5	21	9	22	10	30	58	40	68		145	206	351		100	100	100

TABLE 3 (*Continued*)

L.C.F. (cm)	Gonad Stages													All Stages				Total Beyond Stage 1 (%)			
	1			2		3		4		5		6	7								
	?	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♂	♀	?	♂	♀	Total	?	♂	♀	Total
88				15	84	7	25	4	12	7	26	43	41	70		117	217	334		100	100	100
89				12	59	8	23	2	14	8	13	52	33	72		115	181	296		100	100	100
90				14	54	5	25	5	14	11	15	31	18	56		84	164	248		100	100	100
91				8	12	5	16		17	9	9	12	16	38		50	92	142		100	100	100
92				6	28	2	16	3	15		12	12	13	42		36	113	149		100	100	100
93				9	15	4	9		11	1	15	7	4	27		25	77	102		100	100	100
94				7	20	3	5	2	8		12	6	6	24		24	69	93		100	100	100
95				1	14		6		5	1	4	5	3	10		10	39	49		100	100	100
96				2	8		4		2	2	7	3	7	9		14	30	44		100	100	100
97				2	10	1	3		3		6	1	2	2		6	24	30		100	100	100
98					2	1	6		4		1		2	5		3	18	21		100	100	100
99				1	2	1	1	1	2				4	5		7	10	17		100	100	100
100				1	4		2						2	2		3	8	11		100	100	100
101				1	1		2					1		1		2	4	6		100	100	100
102				1	1				3				1			2	4	6		100	100	100
103					2					1	1					1	3	4		100	100	100
104									1		1			1			3	3			100	100
105											1			1			2	2			100	100
106					2				1								3	3			100	100
107							1										1	1			100	100
108					1					1				1		1	2	3		100	100	100
109																						
110														1			1	1			100	100
111							1				1						2	2			100	100
112							1					1				1	1	2		100	100	100
113																						
114																						
115																						
116														1			1	1		100	100	100
Total	79	345	190	730	1974	211	677	156	449	347	480	1351	1096	1446	79	4236	5216	9531				

cm size-groups from about 55 cm (38 per cent. of both sexes above stage 1) to 64 cm (95 per cent.). The fish which the fishermen prefer and generally take are still larger (see Section IV), i.e. nearly all mature. Only 4 per cent. of those at 70 cm have gonads still at stage 1. It is possible that some of the percentages in the third last column of Table 3 are slightly too low; some observers found it difficult to distinguish stage 1 from stage 2 males and doubtful cases were often classed as stage 1. The total numbers of stage 1 and stage 2 males (third and fifth columns) might be slightly in error — too high and too low respectively — for the same reason.

The total number of fish of all sizes whose gonads were observed was 9531 (Table 3). Females accounted for 54.7 per cent. of this number, males for 45.3 per cent. But an inspection of the numbers at successive lengths shows that the sexes are very nearly equal in fish of all sizes up to 70 cm; the total number of fish of 13 to 70 cm inclusive is 3020, consisting of 1475 females, 1466 males, and 79 of unknown sex. From 71 cm upwards the numbers of females, with only one exception, regularly exceed the numbers of males and do so by increasing margins. This phenomenon has been seen in other fish by various workers (e.g. Fairbridge 1951).

The sex ratios in the groups of fish of different gonad stages, and the actual numbers of both sexes at those stages, are also of interest. The apparent excess of males over females among stage 1 fish is possibly suspect, as noted above. The stages with the largest numbers are stages 2, 6, and 7, i.e. resting, spawning, and spent; stages 3, 4, and 5, i.e. the gonad filling stages, were much less frequently seen among barracouta of either sex. Stage 2 fish are mainly females at all sizes; stage 6 fish (as sampled in these investigations) are almost entirely males; and stage 7 is evenly divided in fish up to about 80 cm, the females predominating at sizes larger than this. The total number of males at stages 2, 6, and 7 combined is 3177 and the corresponding number of females is 3420; males at stages 3, 4, and 5 total 714, females 1606.

It may be concluded that adult males, which are more commonly found at stage 6 or 7 than at any other stage, are sexually active for longer periods than females, in which the commonest gonad stages are 7 and 2.

(*b*) *Spawning Seasons*

According to Table 3 almost all barracouta of 70 cm L.C.F. or over are sexually mature and would be expected to spawn in the spawning season. The changing proportions of gonad stages in these fish at successive times of year in a given area will therefore indicate the general spawning season in that area. Figures 3 and 4 show for different areas and groups of areas (defined in Section I) the percentages of female and male fish with different gonad stages in samples taken in different calendar months; no distinction is made between material collected in different years for the same month.

No difference in spawning season could be detected between areas I, II, and III, between areas VI, VII, VIII, and VIII*A*, or between areas X, XI, and XII, all of which were represented by large numbers of observations spread over several calendar months. For the convenience of the reader the data for these ten areas have been combined into three groups; the original data for each area are available for inspection.

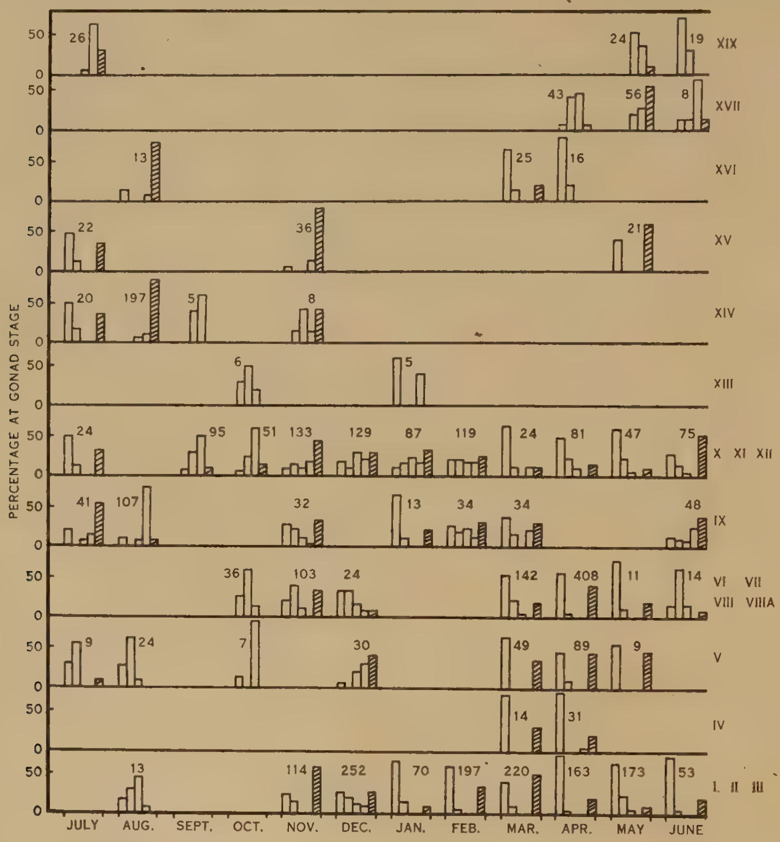

Fig. 3.—Distribution of adult female barracouta gonad stages in samples of different months and areas. The diagram may be understood by referring to the data for December on the lowest line of the figure; the five successive columns from left to right represent the percentages of the available specimens with gonads at stages 2, 3, 4, 5, and 7 respectively; other samples are shown in a similar way, stage 7 being always represented by cross-hatched columns, although all five stages were not represented in every sample. The monthly area samples include fish of 70 cm L.C.F. or over, collected in different years; the total number of specimens examined is shown for each area in each month.

It is convenient to begin with the central part of the Victorian coast, areas X, XI, and XII; there are data for every month of the year except

August, when fish are always very scarce. The gonads of females in these areas are mainly at filling stages 4 and 5 in September and October, although stages 3 and 7 are present. Ovaries at stage 7 (spent) are first

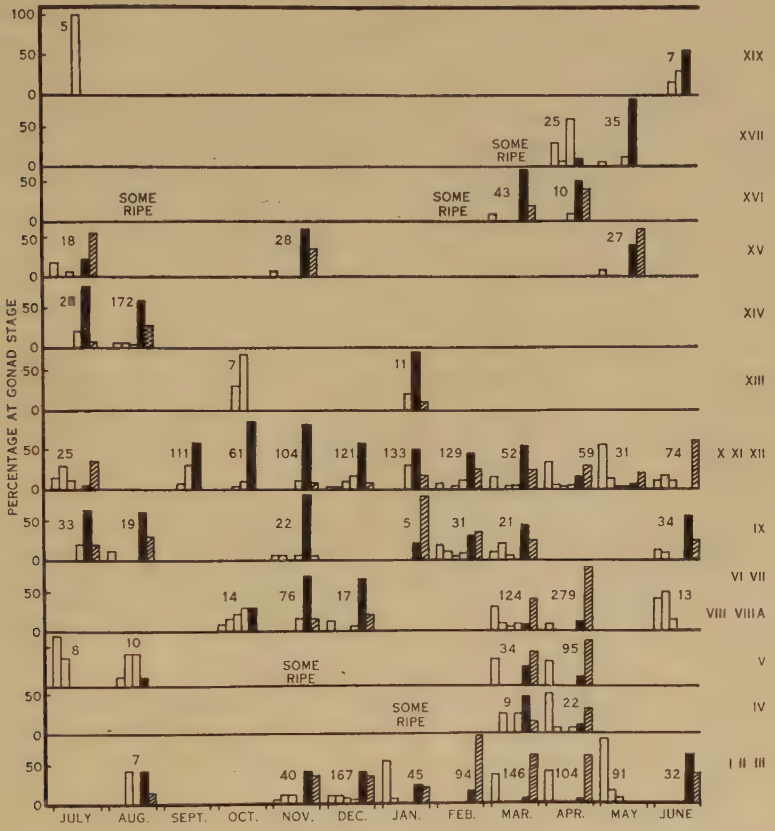

Fig. 4.—Distribution of adult male barracouta gonad stages in samples of different months and areas. The diagram may be understood by referring to the data for December on the lowest line of the figure: the six successive columns from left to right represent the percentages of the available specimens with gonads at stages 2, 3, 4, 5, 6, and 7 respectively; other samples are shown in a similar way, stage 6 being always represented by black columns and stage 7 by cross-hatched columns, although all six stages were not represented in every sample. The monthly area samples include fish of 70 cm L.C.F. or over, collected in different years; the total number of specimens examined is shown for each area in each month; the reference "some ripe" indicates that running ripe (stage 6) males were seen but no other observations on gonad stages were made.

well represented in November when a small proportion at the succeeding stage 2 (recovering) are also found. From then until February all five stages are common. The last stage 5 ovaries occur in March; that is to say, few (if any) fish have yet to commence spawning after that date. The gonads of female barracouta in April, May, June, and July are predominantly spent or recovering (stages 7 and 2) with a few in the early filling stages 3 and 4. Thus the height of the spawning season for females in these areas is from about the end of October to the end of March. The gonads of males on the same part of the coast are predominantly at stage 6 (ripe) from September to March; this stage is less conspicuous in April and negligibly represented in May, June, and July, its place being taken by stages 7 and 2. Stage 5, which was best represented in September, has entirely disappeared by June. Thus the height of the spawning season for males is from about September to April, the males being sexually active for a longer period than the females; but the spawning of both sexes is markedly seasonal.

For the opposite side of Bass Strait, areas VI, VII, VIII, and VIII*A* (northern Tasmania and King I.), there are data for most months from October to June; fish are rarely found in other months. The succession of gonad stages is very like the one just mentioned. Stage 7 ovaries appear in November and stage 5 ovaries are not seen after March; females in April, May, and June are mainly at stages 7 and 2. Stage 6 testes are found from October to April (they may occur later, as data for subsequent months are scanty) but are outnumbered by stages 7 and 2 as early as March; stage 5 is not seen after March. Spawning is definitely seasonal and its peak for both sexes is probably from about the end of October to the end of March, the season being longer for males than for females.

In eastern Tasmania the situation is not very different. For areas I, II, and III there are data for each month from November to June (the normal duration of the fishing season) and a few for August. The female gonads are at early filling stages in August and spawning of females has begun (stage 7 present) by November; stage 5 is not seen after December, stages 7 and 2 predominate from January to March, and stage 2 supplants stage 7 from then to June. Stage 6 males occur from November to June, and even in August (a few only in that month, apparently very tardy or very precocious spawners). Stages 7 and 2 become increasingly represented from January onwards, and stage 5 is not seen after May. Thus females in these areas spawn in November (and possibly earlier) and December; the males spawn for a much longer period although their spawning probably is also seasonal. Observations in area IV were scanty and confined to January, March, and April, but agree well with areas I, II, and III in those months. Area V (Furneaux Is.) is represented in Figures 3 and 4 by data for eight calendar months; there is good agreement with the data for those months for areas I, II, and III.

Thus in the waters of eastern and northern Tasmania, the islands of Bass Strait, and the central part of the Victorian coast, barracouta spawn at about the same season, the height of which for both sexes is approximately from October to March. Females do not spawn in any part of the region from May to August, but a few males can be found in a sexually active condition in each of those months. There may be slight differences in the time of spawning between different parts of the region but it is as yet impossible to be sure of this; the data which suggest such differences might not be perfectly representative of conditions in the various areas and months.

On the east coast of Victoria (area XIV) and in southern New South Wales (area XV) the spawning season is quite different, although the data cover only portion of the year. In area XIV some females have spawned (stage 7) and some are about to spawn (stage 5) in July, August, September, and November, and the same is true of males in July and August (stages 5, 6, and 7 present); these are the only months for which data are available, as there is little fishing in summer and autumn. In area XV the main fishery is likewise in winter and spring and material has been collected in May, July, and November; both males and females spawn in each of these three months. The spawning season in these two adjacent areas therefore covers the winter and spring, at least.

Observations in area XVII (western South Australia) and area XIX (southern Western Australia) were scanty because there is no fishery in those waters. Females in area XVII probably are not yet spawning in April (stage 7 absent, stage 5 rarer than stages 3 and 4) but they are spawning in May and June. Some males in this area are at stage 6 in March and April, but this stage is much more common in May. Thus the spawning season in this area probably does not reach its height until May, and undoubtedly it extends into the winter months. In area XIX there is spawning of females in May and July and of males in June, with indications (high percentages of stage 5 for both sexes in July) that the spawning season extends at least throughout the whole winter. Conditions in these two areas, therefore, are more like those in areas XIV and XV than in the region between.

In area IX (western Victoria) and the adjacent area XVI (eastern South Australia) the observations on the spawning season recall those in both of the adjacent regions — areas XVII and XIX to the west and areas X, XI, and XII to the east. Area IX is represented by material for November, January, February, March, June, July, and August, with stage 7 ovaries and stages 6 and 7 testes occurring in every month and stage 5 ovaries in every month but one. According to local fishermen the winter spawners are consistently larger than the others. There is no fishery in area XVI and the data cover only March, April, and August; stage 6 males and stage 7 females occur in all three months and the former also occur in February.

The small material from area XIII indicates that there is probably some spawning in summer. For areas VIII*B* (western Tasmania) and

XVIII (the South Australian and Western Australian border region) there was virtually no material available for study.

To sum up, there is (*a*) a region about 150 miles from west to east in Bass Strait, from the northern shore to the southern, and extending southwards along the east coast of Tasmania, in which spawning of barracouta is definitely seasonal, being virtually confined to the spring, summer, and autumn months; this distinctly separates two other regions (*b*) to the east in which spawning occurs at least from late autumn to the end of spring and (*c*) to the west in which spawning begins in late autumn and continues well into winter, if not until later; and between (*a*) and (*c*) there is a region (*d*) in which there is some spawning of barracouta in both the warmer and the colder periods of the year. It is not certain that spawning in regions (*b*) and (*c*) is confined to a particular season of the year, but this seems very probable in view of the marked seasonality of spawning in region (*a*). The situation in region (*d*) could mean that the barracouta have two or more spawning seasons a year or spawn all the year round, or that this region is occupied alternately by fish of the adjacent regions (*a*) and (*c*), spawning at the different seasons appropriate to those regions; the latter explanation seems much more reasonable than the former, and adequately covers all the observations in this section and others which are presented subsequently (Section V(*b*)).

These four regions — one of "summer spawners," two of "winter spawners," and one of both kinds of spawners, are indicated in Figure 1; the approximate southern boundary of winter spawning is lat. 38° 30′ S. The spawning season in region (*b*) clearly overlaps that of (*a*) in the spring months, and the same might, for want of evidence to the contrary, be true of the season in region (*c*); but it is clear that there is some segregation of at least three different breeding groups of barracouta in Australian waters. It is reasonable to conclude that there are at least three different, although not necessarily discrete, populations of the fish in those waters; it is shown subsequently that the number probably exceeds three.

(*c*) *Feeding Seasons*

Most of the barracouta whose sex and maturity stages were recorded were also examined for signs of food in the stomach. It is intended to describe and analyse the results of this study in a later paper but a few matters are of interest at this stage. The principal food of the barracouta in south-eastern Australian waters is the euphausian *Nyctiphanes australis* Sars. Other prey organisms include small fishes of many species (including the anchovy, *Engraulis australis* (White), and the young of the barracouta itself), other planktonic crustaceans, and small cephalopods.

Figure 5 shows the percentage of stomachs of barracouta 70 cm or more in length (i.e. sexually mature) which contained any food for each month in each area for which data were available; some areas have been grouped in the same way as in Figures 3 and 4, and no distinction is made between observations made in different years or between the sexes. Captured barracouta are occasionally seen to disgorge food on deck; therefore some of the percentages in Figure 5 may be too low but the errors are probably not serious. Of the total of 6099 stomachs represented in Figure 5, 39 per cent. contained food.

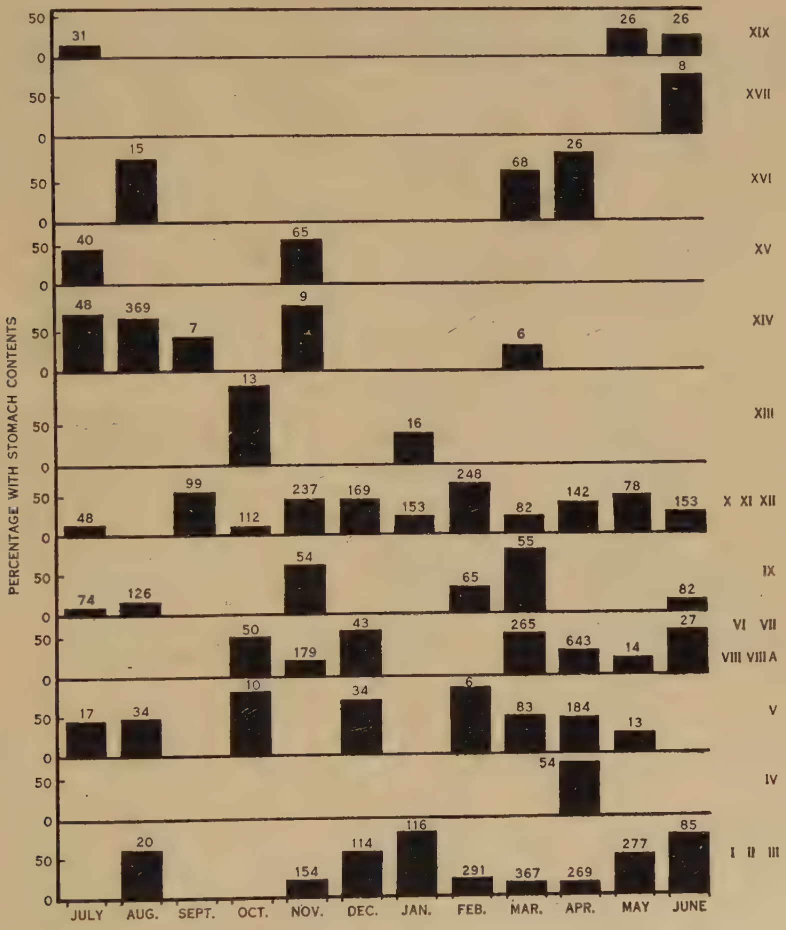

Fig. 5.—Percentages of adult barracouta with food in the stomachs in samples of different months and areas. The monthly area samples include fish of both sexes of 70 cm L.C.F. or over, collected in different years; the total number of specimens examined is shown for each area in each month.

The variation in percentage of barracouta containing any food, from month to month and area to area, gives no clear picture of the feeding habits of the species. That is indeed the main interest which attaches to Figure 5, as there might, on the other hand, have been some regular waxing and waning of feeding activity according to season. Hart (1946) remarked of this species: "The relative scarcity of *Thyrsites* in winter and early spring (the spawning period) is attested by returns from all the countries where it is regularly fished. This is doubtless partly due to a slackening of feeding intensity, well known amongst most fishes when spawning, that will obviously tend to reduce catches of line-caught species; but some definite migration for spawning purposes may also be involved." It was shown in the previous section that the winter and early spring is not the spawning period in all Australian waters; and it is shown below in Section V(*a*) that barracouta are not uniformly scarce in Australian waters at that time of year or any other, and that whenever the spawning season occurs in any area it is also a season at which barracouta are plentiful. Furthermore it is clear from Figure 5, referring also to Figures 3 and 4, that there is no marked diminution of feeding during any spawning season; most of the samples which contained a high proportion of fish with food in their stomachs were taken during spawning seasons, although other samples of those seasons contained relatively few feeding fish.

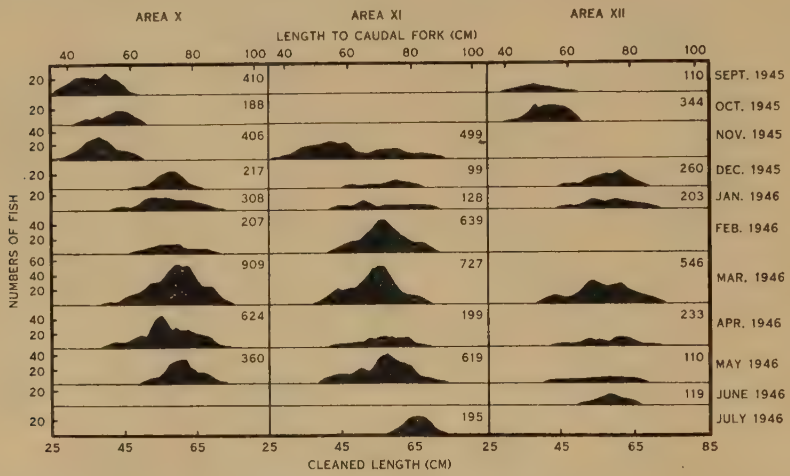

Fig. 6.—Length frequency polygons for barracouta samples of different Victorian areas in successive months of 1945-46. The numbers measured are shown to the right of the polygons.

The barracouta in Australian waters probably takes any suitable food whenever it is available. Until a more detailed study of the principal prey species is made it would be injudicious to attempt to base any more definite conclusions on the data presented, which merely show that the feeding behaviour of the barracouta is not as simple as has been thought.

IV. Size Composition of Catches

There is some evidence, from the mass recording of fish-lengths in random samples of commercial catches, of rather consistent likenesses and differences in the size composition of groups of barracouta available in different fishing areas.

The results of this measuring in the years in which most of it was done are summarized as length frequency polygons (data smoothed by moving average of three) in Figures 6-9. The methods of measuring and conversion of measurements were described in Section I.

Figure 6 summarizes 8659 measurements from areas X, XI, and XII in the fishing season of 1945-46. The monthly sample numbers are small (similar monthly samples have been omitted in Figs. 8 and 9) but the sampling was even and covered most months in the three areas. These measurements were made in the Melbourne Fish Market; it was impossible to obtain further data there in subsequent years.

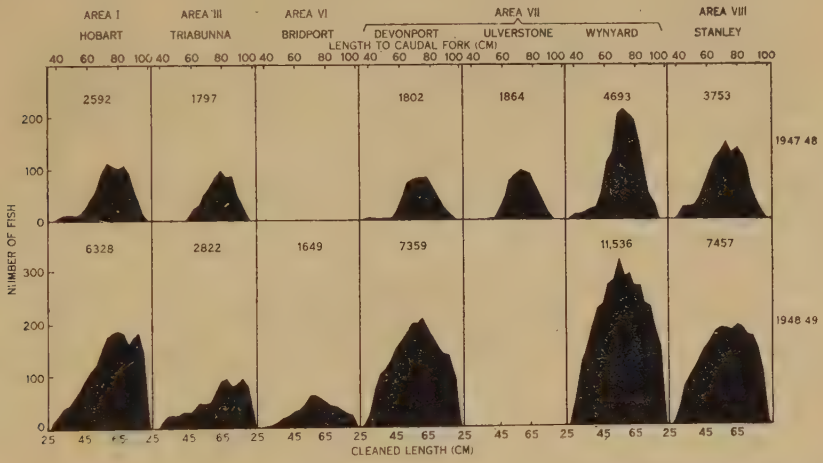

Fig. 7.—Length frequency polygons for barracouta samples of different Tasmanian areas in 1947-48 (upper series) and 1948-49 (lower series). The numbers measured are shown above the polygons.

Figure 7 depicts measurements from areas I, III, VI, VII, and VIII in the fishing seasons of 1947-48 (upper panels; 16,501 measurements in all) and 1948-49 (lower panels; 37,151 measurements in all). Except for a few taken by research vessels, all the fish were measured at the factory of International Canners Pty. Ltd. at Ulverstone, Tas., which received barracouta from most Tasmanian ports. Unfortunately the measurer was uncertain about the dates of capture of many samples and the data could not be dissected according to months. Probably there was fairly even sampling from month to month.

Figure 8 presents similar data for 38,040 fish from areas X, XI, XII, and XIII in various months in the 1951-52 season, and Figure 9 summarizes 31,203 measurements from areas VII, X, and XII in the 1952-53 season. The fish were measured at the ports by investigators who visited them as often as their other duties would permit.

In these length frequency polygons there is much variation in the numbers at 35-65 cm (L.C.F.) relative to the numbers of larger fish. There seem to be at least two age-groups within this range, the senior one with mode at 55-60 cm being the better represented (Figs. 6, 8, 9). These small fish occur in the samples of each area (except area XIII which was sampled only once), of each year, and of almost every month. There are differences in their representation between areas (e.g. proportionately fewer in eastern Tasmanian samples than in those from Bass Strait) which may be due to different types of fishing, and there are differences between

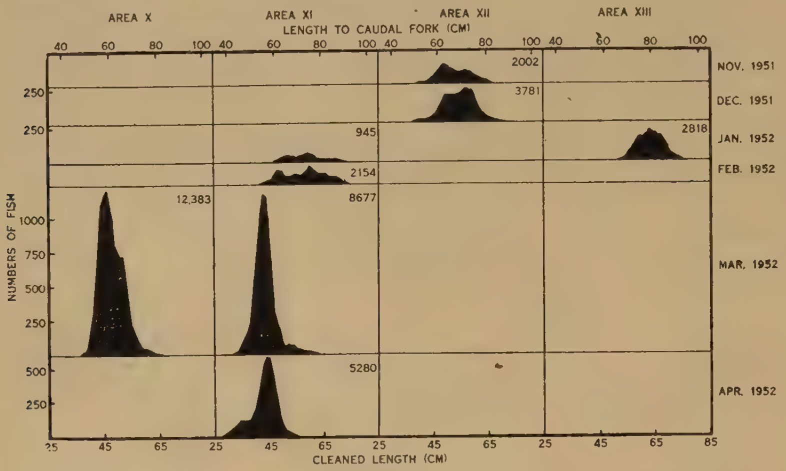

Fig. 8.—Length frequency polygons for barracouta samples of different Victorian areas in successive months of 1951-52. The numbers measured are shown to the right of the polygons.

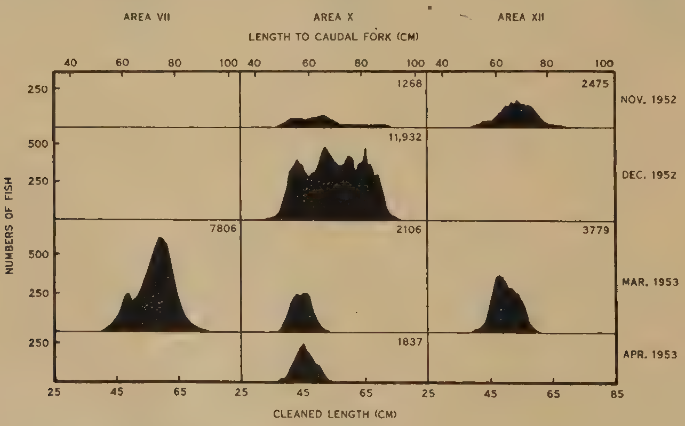

Fig. 9.—Length frequency polygons for barracouta samples of different Victorian and Tasmanian areas in different months of 1952-53. The numbers measured are shown to the right of the polygons.

years (e.g. proportionately more abundant in northern Tasmanian samples in 1948-49 than in 1947-48) which may be due to variations in the numerical strength of year-classes (Fig. 7); it is hoped to investigate these matters at a later date. Even more striking is the fact that the small fish are much better represented in the samples of the early and late months of the fishing season than in the middle months, at least on the Victorian coast (Figs. 6, 8, 9). This can be explained by the fact that the fishermen definitely prefer the larger, sexually mature barracouta and select them when they are available; but these larger fish are migratory (see Section V(*a*) below) and thus not always plentiful at the beginning and end of a season, and when this is so the catchers will take the smaller, mainly virgin, barracouta of the recruit groups, which appear to have a longer season in the coastal waters.

It is therefore desirable to ignore the fish below about 65 cm when using these polygons as indicators of the general size composition of the groups of barracouta available in different regions and years; the polygons provide valid evidence of size-composition of groups of mature fish only. The following observations can be made about the sizes of mature fish:

1. Victorian barracouta (areas X, XI, XII, XIII) in each of three fishing seasons (1945-46, 1951-52, 1952-53) averaged between 70 and 80 cm L.C.F. The proportion over 90 cm was insignificant (Figs. 6, 8, 9).

2. Northern Tasmanian fish (areas VI, VII, VIII) in each of three seasons (1947-48, 1948-49, 1952-53) averaged between 70 and 80 cm. The proportion over 90 cm was insignificant in two seasons but quite substantial in 1948-49 (Figs. 7, 9).

3. Eastern Tasmanian fish (areas I, III) in each of two fishing seasons (1947-48, 1948-49) averaged between 75 and 85 cm. The proportion over 90 cm was substantial in both seasons (Fig. 7).

4. In each of the two seasons for which there are eastern Tasmanian data, the length frequency polygons for areas I and III are very similar. In each of the two seasons for which there are data from more than one area of northern Tasmania, the polygons for the different areas are likewise very similar (Fig. 7). The size composition of the catch was similar in the separate Victorian areas X, XI, and XII in the 1945-46 season (Fig. 6), although the data are not copious; the Victorian measurements in the other two seasons do not appear to represent the entire season so well in any area (Figs. 8, 9).

5. The size composition of the groups of barracouta in eastern and northern Tasmania can be compared for the same fishing season 1947-48 and again in 1948-49. The difference between the eastern and northern fish is marked, but yet is not so great or constant as to indicate segregation of different age-groups of a single population (Fig. 7). In 1947-48 the

modal size of northern Tasmanian fish was about 70 cm and that of eastern Tasmanian fish about 80 cm, but in the following year the modes were respectively about 70 and 90 cm. Data on average weights of headless cleaned barracouta in these two regions in two other years show a similar kind of variation. In 1941-42 and 1942-43 Tasmanian fishermen listed catches in their official catch returns both by total weight and number of dozen fish (Blackburn 1950); mean weights per dozen in 1941-42 were 56 lb in areas I, II, and III and 41 lb in areas VII and VIII, a difference of 1 lb 4 oz per fish, but in 1942-43 the respective mean weights were 49 and 46 lb, a difference of only 4 oz per fish. It is common knowledge in the Tasmanian fishery that eastern barracouta are longer and heavier, on average, than northern, but the difference is not constant.

6. A similar comparison of Victorian and northern Tasmanian fish can be made for only one season, 1952-53. Approximately 12,000 measurements of mature barracouta, representing four monthly samples from two Victorian areas, can be compared with about 6000 measurements representing one monthly sample from one northern Tasmanian area (Fig. 9). These data are probably not as representative of the groups of fish in the two regions for the entire season as are those of Figure 7. Nevertheless they indicate that in each region the average size of the fish was about 70-75 cm and that there were very few over 90 cm. The measuring programmes of 1951-52 and 1952-53 were disrupted by shortages of mature fish, as both seasons were poor on both sides of Bass Strait (see Section V(*a*) below).

It is therefore very probable that the barracouta of south-eastern Tasmania belong to a single population and those of northern Tasmania to a different one, although the two populations are not necessarily quite discrete. And it is possible that the barracouta of the central part of the Victorian coast belong to a single population which may be the same as that to which the northern Tasmanian fish belong. That is to say, even the barracouta which spawn in the warmer months of the year in Victorian and Tasmanian waters (see Section III(*b*)) can be divided into two different populations. The fact that the average size of fish is larger in eastern Tasmania than in Bass Strait might, taken by itself, suggest merely some segregation of the larger fish of a single population of the whole region; but the difference in size is not constant, is sometimes very small, and is never so great as to suggest that large fish cannot find tolerable conditions in Bass Strait (e.g. see Fig. 7, 1948-49 data for areas VI, VII, and VIII). The differences in size composition of catches in eastern and northern Tasmania are probably due to the passage of year-classes of differing numerical strengths through two different populations, one of which has a higher growth rate or a lower mortality rate than the other; see Section VII on the possibility of a lower mortality rate in the population of eastern Tasmania.

V. AVAILABILITY: SEASONAL AND ANNUAL CHANGES

(a) *Victoria, Tasmania, and New South Wales*

Blackburn (1950) discussed the reliability of records of barracouta catches available for the three States which have a fishery. He also studied changes in availability of fish to the catcher at the principal Victorian fishing ports by dividing annual total catches by the numbers of fishing boats licensed in those years. This was not entirely satisfactory because all boats do not fish for barracouta and the fish are not caught all the year round, and there was no information at all about fishing effort for barracouta in Tasmania and New South Wales. One important point which emerged was that the curve of catch per boat from year to year closely parallels the curve of total catch. Better estimates of effort are now available for most areas for the last few years and many important conclusions can now be drawn from catch and effort records. Tables of these records have been omitted from this paper because of their length; the information in them is summarized in Figures 10-14.

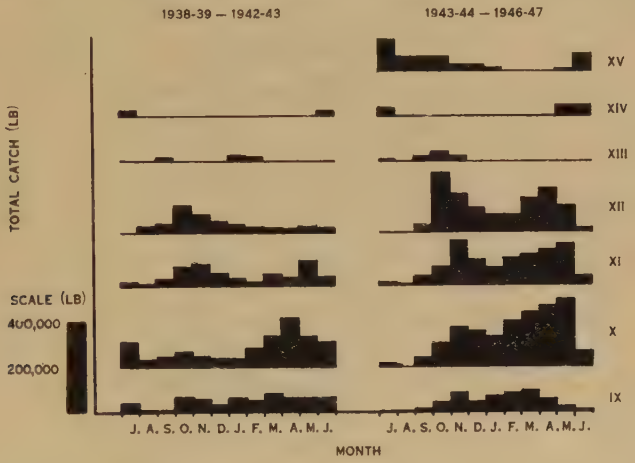

Fig. 10.—Mean barracouta catches for the calendar months over the 5 yr 1938-39 to 1942-43 and the 4 yr 1943-44 to 1946-47, for Victorian and New South Wales areas numbered at the right.

It is convenient to recognize four periods in the history of the barracouta fisheries as regards availability of records of catch (beheaded and cleaned fish) and effort.

(1) 1911 to 1937-38.—Records of total catch by months and areas are available for Victoria, where areas IX (mainly Port Fairy) and XI (mainly Queenscliff) contributed over 80 per cent. of the catch. Records of total catch in Tasmania are only available for a few years and even then are estimates (Blackburn 1950) and are not dissected by months and areas. No records are available for New South Wales but catches are

known to have been negligible. There are no good records of fishing effort.

(2) 1938-39 to 1942-43.—The position is much the same except that the Victorian catches were more evenly distributed along the coast, areas X (mainly Apollo Bay and Lorne) and XII (mainly San Remo) having become important (Blackburn 1950, Tables 3, 4). There are reliable dissected records of Tasmanian catches for two years only (Blackburn 1950).

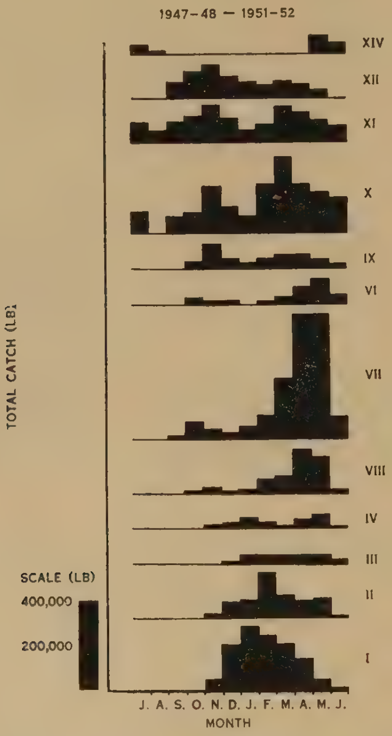

Fig. 11.—Mean barracouta catches for the calendar months over the 5 yr 1947-48 to 1951-52, for Tasmanian and Victorian areas numbered at the right.

(3) 1943-44 to 1946-47.—A significant fishery began in New South Wales and records of total catch by months and areas are available. The position is otherwise unchanged.

(4) 1947-48 to 1951-52.—Trustworthy records of total catch by months and areas are available in Tasmania, where the practice of reporting catch by weight had almost completely replaced the inconvenient practice of reporting by number of fish. Good records of fishing effort are to hand from Victoria (from 1948-49) and Tasmania, where the

number of boats contributing to the barracouta catch of each area in each month was recorded for the first time. There are no such effort records for New South Wales where the fishery had again become unimportant, although dissected records of total catch are available.

The New South Wales records show that nearly all the catch is taken in the far south of the State, especially near Eden. Thus area XV, defined above as the whole of New South Wales, may be regarded as the Eden area for purposes of this section of the paper.

Figure 10 shows on the left the average catch per calendar month over the period 1938-39 to 1942-43 in each Victorian area, and on the right similar information for the period 1943-44 to 1946-47 in each Victorian area and in area XV.

These histograms show that in areas IX, X, XI, and XII there is a spring peak (October-November) and an autumn peak (March-May) in the catch of barracouta, summer catches being lower and catches in winter (July-September, especially August which is generally the poorest month of the year) much lower still. In area XII the spring catch is greater than the autumn catch, in area X it is the converse, and in areas XI and IX the two are comparable. The spring peak tends to be earlier in the east (area XII) than in the west (area IX) and the autumn peak earlier in the west than in the east, the peaks in the intermediate areas tending to be intermediate in time. The two peaks are thus closest in point of time in area IX, where they are also least distinct from the level of summer catch.

Little fishing occurs in area XIII, where the fishing ports in Corner Inlet are some distance from the open sea and it does not pay the fishermen to go out for barracouta unless they are especially plentiful or command an unusually high price. There is significant fishing sometimes in early spring, less often in summer, and very infrequently in autumn; this distantly resembles the situation in the adjacent area XII in the period 1938-39 to 1942-43, i.e. before it became an important fishing locality. In areas XIV and XV the situation is quite different and is discussed below.

In Figure 11, which shows the average catch per calendar month in the same way as Figure 10 for the 5-yr period 1947-48 to 1951-52, the same features are apparent. Figures on catch per boat per month are available for most areas in this period, and could have been used instead of the figures on total catch. The latter were used to facilitate comparison between the period 1947-48 to 1951-52 and the two earlier periods, for which there are no data on numbers of boats. It is permissible to use such figures on total catch to indicate changes in the availability of fish because variations in total catch and catch per boat run closely parallel from month to month in these fisheries; this is clearly shown in Figures 12 and 13, which show respectively the total catch and catch per boat in each month of each of the 5 years 1947-48 to 1951-52, in each area in which there were significant fishing operations. Catches in areas V, VIII*A*, VIII*B*, XIII, and XV were too small to be shown on the same scale in these figures or in Figure 11. Figures 12 and 13 also show the spring and autumn peaks in the histograms of each year, although naturally not as clearly as in the 5-yr averages in Figures 10 and 11.

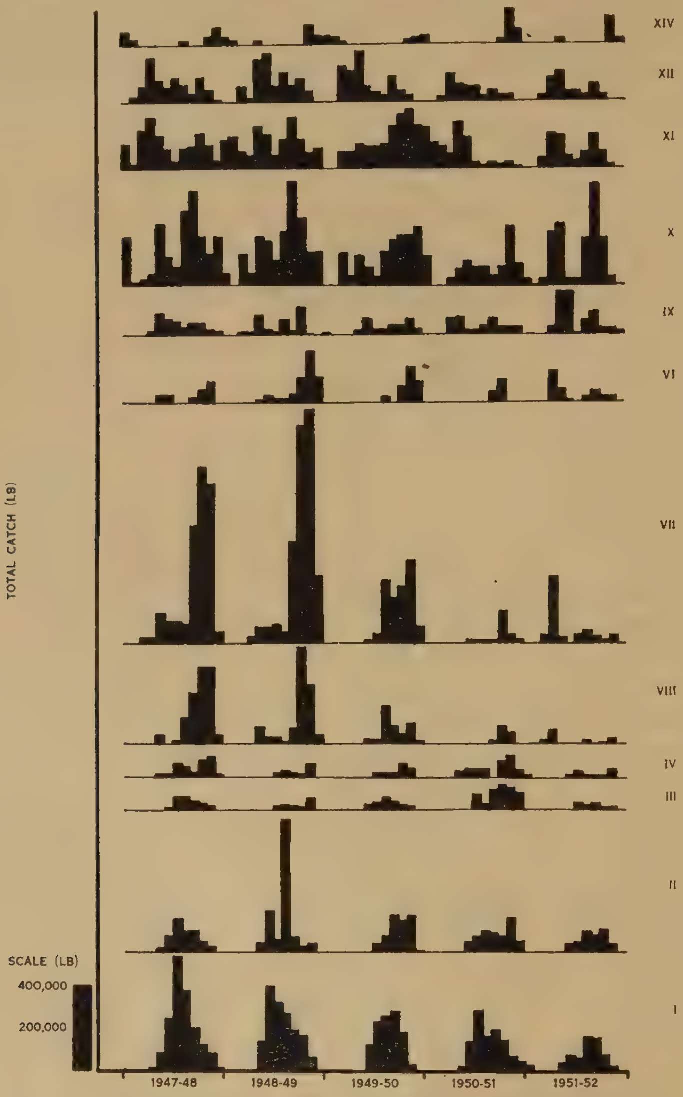

Fig. 12.—Barracouta catches for successive months over the 5 yr 1947-48 to 1951-52, for Tasmanian and Victorian areas numbered at the right.

It should be explained that there is some fishing effort expended in almost every month in every area, even in the months which are represented by small or almost nil catches in these figures, so that the seasonal changes in availability of fish which are apparent in Figures 10 to 13 are quite real (except possibly to some extent in area XIII as noted above, and in areas XIV and XV as noted below). There are actually a few fish to be caught in almost every month and even when they are scarcest (catches too small to be shown in Figs. 10-13) the price is often correspondingly high, sufficient to repay the output of fishing effort. Many of the boats, especially on the Victorian coast, are suitable for little but

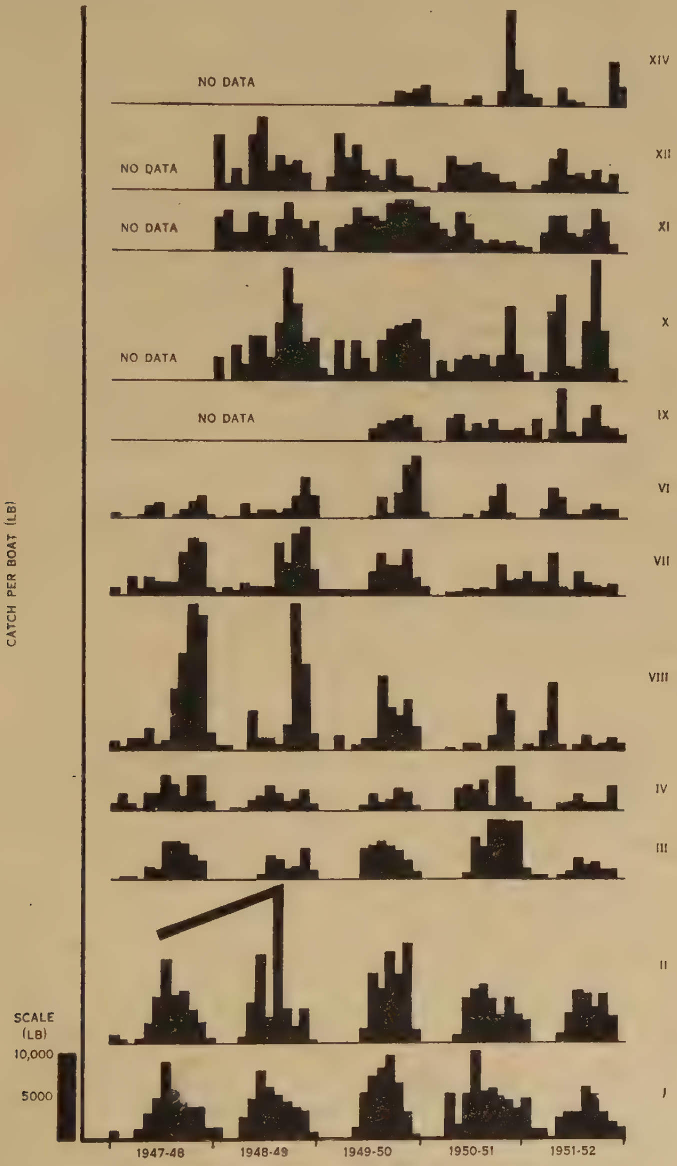

Fig. 13.—Barracouta catches per boat for successive months over the 5 yr 1947-48 to 1951-52, for Tasmanian and Victorian areas numbered at the right.

barracouta fishing and their owners do as much of that as possible, even at times of scarcity or adverse weather conditions; and the better boats which may engage in other forms of fishing (i.e. for shark, crayfish) must catch a supply of barracouta for bait before they can do so; thus in area XI, where the fish are normally scarce in winter, their presence in unusually good numbers in the winter of 1950 was not overlooked by the barracouta fishing fleet (Figs. 12, 13).

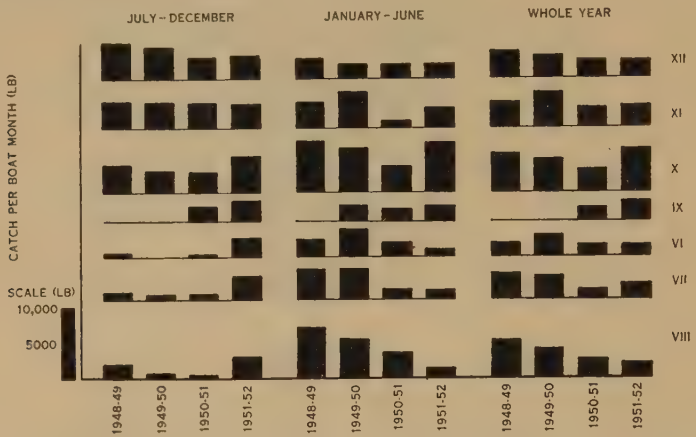

Fig. 14.—Barracouta catches per boat-month for the period July-December, for the period January-June, and for the whole year, in the 4 yr 1948-49 to 1951-52, for Tasmanian and Victorian areas numbered at the right.

It was shown in Section III(*b*) that the spawning season in areas X, XI, and XII is virtually the same, approximately mid spring to early autumn, and that this is also a spawning season in area IX. The season of greatest availability of barracouta on this part of the Victorian coast is thus mainly a spawning season. Since barracouta are capable of travelling considerable distances (Section II) it follows that none of the fish in these four areas are reproductively isolated from the others. No other possible isolating mechanism is obvious either. The length frequency data of Section IV showed that the barracouta of these areas might be all of the same population, and this is demonstrated beyond reasonable doubt by the data on seasonal availability just presented. The most reasonable explanation of the spring and autumn peaks, and their tendency to appear in successive localities at successive dates, is as follows. The barracouta of the southern coast of Victoria all belong to the same population, the main body of which appears first in the eastern part of the region and moves gradually westward towards the South Australian border (and probably beyond, see following Section V(*b*)) during the spring and early summer, returning in the late summer and autumn. The westward movement is a spawning migration, although the fish do not cease feeding (Section III(*c*)); on the return migration some fish are still spawning and many are feeding.

Not all fish necessarily move or move at the same time or to the same extent, and some may move in the opposite direction to the main body. Of the three fish which were tagged in this region and for which there is accurate information about recapture, one appeared to have remained in area XI for 2 months during the height of the spring migration; one either overwintered in area XI or returned to it in the following spring; and one moved slightly to the east in its 2 wk of freedom during the height of the spring migration (Section II). The third fish may have been making an early return movement eastwards, a brief eastward deviation before resuming its westward migration, or an entirely abnormal movement as a result of being tagged.

On the other side of Bass Strait the situation is remarkably similar, as shown by Figures 11-13. In areas VI, VII, and VIII there is in each year a spring and an autumn peak in the availability of barracouta, the summer being somewhat less productive and the winter very poor. In most years the spring peak is much lower than the autumn one, somewhat as in area X, but this was reversed in 1951-52. Again there is a tendency for the spring peak to occur later in the west than in the east of the region and the autumn peak later in the east than in the west. In these areas too it was noticed previously that the spawning seasons are all the same, from about mid spring to early autumn (and also in area VIII*A*, further west, where there is no fishery), so that the conclusions which were reached about the northern side of Bass Strait apply equally to the southern. There is a spawning migration from east to west and subsequent return movement. The only difference is that the spawning migration seems to involve far fewer fish than the return movement in most years. This probably means that on the Tasmanian north coast the fish are mainly well off shore, beyond the small seawards range of the barracouta fleet, in spring although not in autumn; the low autumn peak in area XII is possibly to be explained in a similar way.

The question that now arises is whether the barracouta of southern Victoria and northern Tasmania, which behave in an identical way at the same seasons, belong to the same population.

The two groups are sometimes in contact. This is shown by the fact that research vessels have taken barracouta continuously while on passage across the eastern and western ends of Bass Strait, i.e. between Wilson's Promontory, the Furneaux Is., and Cape Portland and between Cape Otway, King I., and the Hunter Is. (Fig. 2). There is no similar evidence of continuous occurrence of the fish across the central part of the Strait and it is possible that the barracouta avoids waters such as these which are a long distance from any land, although it is quite capable of crossing them (Section II); and although its food *Nyctiphanes australis* has been taken plentifully in plankton nets in the middle of the Strait in the barracouta season. The fact that fishermen do not catch barracouta in these areas is not significant because they hardly ever try to; the barracouta fleets use no ice and land their fish the same day (generally the same morning or afternoon) as they are caught, which means that their operations are confined to waters near the fishing ports. The research ship *Endeavour* trawled barracouta about 30 miles south-west of Wilson's Promontory in October 1909 (Dannevig 1910, pp. 16, 30, 42, see Haul 137; position marked in Fig. 2 of the present paper) and the authors know of no authentic record of the occurrence of the fish any further off shore in the central basin of Bass Strait. Nevertheless barracouta might occur in this area, and even if they were entirely absent it would not invalidate the hypothesis of a single population of fish in the Strait. Even if the two migration streams of fish were entirely separate, they might have identical winter quarters and intermingle there.

Further, there is other evidence of likeness between the northern and southern Bass Strait fish. The size composition in the two groups is similar (Section IV), and another interesting piece of information can be obtained from the catch and effort data. Figure 14 shows the mean catch per boat-month for each numbered area in Bass Strait, separately for the periods July to December (the spring peak) and January to June (the autumn peak) in each year from 1948-49 to 1951-52: e.g. the number of boats which fished an area in July was added to the number which fished it in August, and to the corresponding number in September, and so on to December to obtain the total number of boat-months of fishing effort expended in the area for the half-year; the half-yearly catch for the area was then divided by this number of boat-months. As noticed above, the spring and autumn peaks are characteristically high or low in some areas, a fact which has to be borne in mind when areas are being compared. Allowing for this, the following conclusions may be drawn from Figure 14.

The spring peak of 1951-52 was the best of all four in areas X (Victoria) and VI, VII, and VIII (Tasmania). The same might have been true of area IX (Victoria) for which there are data for 2 yr only. It probably was also true of the Victorian areas XI and XII although Figure 14 does not suggest it, because fishermen and market agents stated at the time that the market was glutted and that catch "limits" had been imposed on the fishermen of those areas. This spring was recognized as a notable one by both Victorian and northern Tasmanian fishermen.

The autumn peak of 1950-51 was lower than the preceding two in areas XI and X (Victoria) and in the three Tasmanian areas. In area IX (Victoria) it was lower than the peak of the preceding year, there being no data for the year before that. Only area XII, where there was little change from year to year, was distinctly different. The autumn peak of 1951-52 was also poor in areas XI, VI, VII, and VIII, although in some of these areas it was not as poor as the previous one. In area IX this peak was a little better than the preceding one. In area X the availability of barracouta appears from Figure 14 to have been a great deal better in 1951-52 than in 1950-51; but this was probably not true of migrating adult fish in view of the data of Section IV (Fig. 8) which show that most of the catch consisted of juveniles, the more preferred fish being scarce. Thus again it was only in area XII that the availability of autumn fish was normal; and there the normal is rather low.

It may therefore be said that the availability of barracouta fluctuated in a very similar way in most parts of Bass Strait in which it was fished, on the Victorian coast as well as the Tasmanian, during the years 1948-49 to 1951-52. The first 2 yr were better for the fishery than the two following: in these latter two the autumn availability was almost everywhere low, although in one year this was partly compensated for by a good spring in most and probably in all areas. In fact these changes were quite obvious at the time they occurred, to the fishermen and to investigators who visited the ports; and to judge from such visual and anecdotal evidence (catch and effort records not yet being available) the autumn of 1952-53 was like the previous two on both sides of the Strait.* These changes are further discussed in Section VII.

Thus all the available evidence makes it highly probable that the barracouta in Bass Strait and its western approaches belong to one population. The final proof which could come from tagging has not been obtained, but there have been so few recaptures of tagged barracouta anywhere that this fact is not significant. Whether or not this population extends across the middle of Bass Strait during the fishing season is not known. In any event the fish probably occur further off shore than the fishermen go at certain times and in certain places, e.g. in the spring of most years on the north coast of Tasmania. The bulk of the population normally vacates Bass Strait in winter, disappearing towards the east — more particularly towards the south-east, to judge from the relatively low autumn availability in area XII.

In the waters to the north-east of Bass Strait (whose eastern boundary is regarded in this paper as the Wilson's Promontory-Furneaux Is.-Cape Portland line) there appears to be a different population. Figures 10-13 show that there is only one important fishing season in area XIV and that its peak is in winter (May-July); occasionally a few fish are caught from November to February (Figs. 12, 13, especially for 1951-52). Most of the fishing in this area is off Lakes Entrance (Fig. 2). Further north in area XV (southern New South Wales) the situation is not very different; the winter peak is a little later and appreciable but diminishing captures continue to January (Fig. 10). As in Bass Strait, the fishing season in these areas is a spawning season, spawning occurring from late autumn to late spring (Section III(*b*)), although the fish also feed at this time (Section III(*c*)). A barracouta tagged just east of Flinders I.

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* This has now been confirmed from catch and effort records.

(Furneaux Group, area V) in early April was recaptured in the middle of the following August in the eastern part of area XIV, and samples taken in those two areas in those two months were remarkably similar in size composition (Section II).

The most reasonable explanation of all these facts, taking also into account the conclusions previously drawn about the behaviour of barracouta in Bass Strait, is that there is a spawning migration in winter from the Furneaux Is. northward through waters adjacent to the east coast of Victoria into New South Wales, and that the fish return southwards during the spring and summer. The only difficulty about this hypothesis is that barracouta appear to be scarce in area XIV in the late spring and early summer when a second peak of availability, representing the return movement southwards, would be expected. But some reports from fishermen in this area suggest that there would be no demand for spring or summer barracouta from those waters even if they did catch them, as the demand at the Melbourne market is limited and can generally be met by fishermen from nearer ports (areas X, XI, and XII) in the warmer months, and this might explain the fact that so few are caught. On the other hand the fish might move southwards at too great a distance from the shore for the fishermen to encounter them. In any event it is significant that some fish are taken in this area in late spring and summer in some years — fewer than in winter, but more than in early spring. The occasional summer captures in area XIII (Fig. 10) may be fish of this population, in part or whole.

Measuring of barracouta in these areas has not been on a large scale but there are indications that the fish are of larger average size than those in Bass Strait. The largest barracouta noted in these investigations (116 cm L.C.F.) was taken in area XIV. An indication of the mutual isolation of the two populations, apart altogether from the great difference in spawning season, is provided by the catch and catch per boat data for area XIV in Figures 12 and 13. The winter season of 1951 was much better than the previous season, whereas the autumn season of 1951 in Bass Strait was unusually poor.

On the east coast of Tasmania (areas I-IV) the fishing season is nearly the same as in Bass Strait but it generally starts later, in late instead of early spring, and extends to about the end of autumn (Figs. 11-13). The spawning season is likewise much as in Bass Strait, probably but not certainly a little later (Section III(*b*)), and it is necessary to look further for indications that the fish of the two regions belong to different populations. Good evidence of this from length frequency data has already been presented (Section IV). Further evidence is available from the catch per boat per month figures summarized in Figure 13, which show that availability of barracouta in the fishing season as a whole was about the same in each of the four seasons 1947-48 to 1950-51 but distinctly lower in 1951-52, in each of the four areas*; it will be recalled that the annual changes in availability in Bass Strait and area XIV were quite different.

There are indications that fish of this east Tasmanian population migrate within the fishing season. The series of histograms for areas I, II, and III hardly ever show two distinct peaks in a season, but those of area IV, further north, do so very regularly. In this area the earlier peak occurs about December-February and the later one about April-May. In areas I-III the best fishing months are January-March. The situation in area IV is thus like that in areas XII and XI and the situation in areas I-III, where availability is more even from month to month, recalls that in areas IX and XV. The recapture in area II, late in March, of a fish tagged 6 wk previously in area III (Section II) shows that fish move appreciable distances along the coast. From these observations and from what has been shown about the behaviour of barracouta in other areas it may be concluded that there is a tendency for the fish to move down the east coast of Tasmania in the summer and back in autumn, disappearing (as do the other two populations in their respective off seasons) towards the Furneaux Group. As in the other populations, the first phase of the migration would appear to be a spawning movement, although the fish feed at the same time (Section III(*b*),(*c*)).

If there were no migration the pattern of availability from month to month for area IV should resemble that for areas I, II, and III, i.e. there should be only one seasonal peak in all areas. If migration took place in the opposite directions to that postulated above, i.e. from south to north and back, one would expect two well-marked seasonal peaks of availability in area I (and perhaps in areas II and III) instead of in area IV; and it would follow that the winter quarters of these barracouta were probably near the south of Tasmania, where winter water temperatures are below the level preferred by the fish (see Section V(*c*) below).

No worth-while information about barracouta is available from the west coast of Tasmania (area VIII*B*). The region is sparsely inhabited and deficient in fishing havens and very little fishing of any kind is done. There are reports of captures of barracouta in summer and as the latitude is high that is probably the spawning season for the area (see Fig. 1). The fish that occur there may belong to the Bass Strait or east Tasmanian population or both, or they may be an entirely different group.

(*b*) *South Australia and Western Australia*

There is no commercial fishery in these States and knowledge of the distribution of barracouta is based mainly upon observations made from research vessels from time to time, usually in the course of other work.

Figure 15 summarizes this information for South Australian waters (areas XVI, XVII). Observations are lacking for September, October,

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* Availability was again normal in 1952-53 (from catch and effort records for that year).

November, January, and July. No barracouta were seen in December. In February they were abundant in area XVI but none were seen in area XVII. In March they were again abundant in area XVI and present, but scarce, in area XVII. In April they were somewhat scarcer in area XVI and plentiful in area XVII. Area XVII was also good for barracouta in May, when area XVI was not examined. The available observations for the winter months (June and August) have been combined in the sixth panel of Figure 15. The June observations were brief, but revealed the presence of fish in both areas. The August work was confined to area XVI, where barracouta were found.

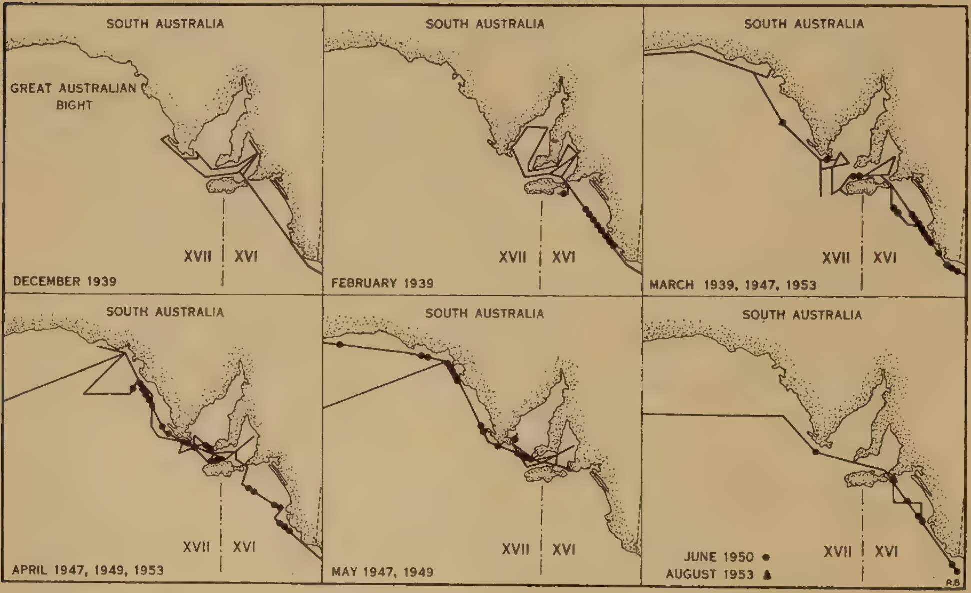
SOUTH AUSTRALIA
GREAT AUSTRALIAN BIGHT
XVII
XVI
DECEMBER 1939
SOUTH AUSTRALIA
XVII
XVI
FEBRUARY 1939
SOUTH AUSTRALIA
XVII
XVI
MARCH 1939, 1947, 1953
SOUTH AUSTRALIA
XVII
XVI
APRIL 1947, 1949, 1953
SOUTH AUSTRALIA
XVII
XVI
MAY 1947, 1949
SOUTH AUSTRALIA
JUNE 1950 ●
AUGUST 1953 ▲
XVII
XVI
RB

Fig. 15.—Movements of research vessels in South Australian waters in different calendar months, showing localities in which barracouta were caught.

The meaning of these observations becomes clearer when reference is made to the sexual condition of the fish (Section III(*b*)). Those taken in area XVI in February, March, and April were in spawning, near spawning, or spent condition, like those which are taken in Victorian waters at the same season; but in area XVII most of the March and April specimens had not yet spawned and gonad stages 6 and 7 were not well represented until May. There appear, then, to be two groups of barracouta in South Australian waters in the autumn months: one east of about long. 137° 30′ E., well represented and spawning at least as early as February and as late as April; and the other further west, not well represented until April, and not actively spawning until May.

The eastern group is almost certainly part of the Bass Strait population. It is adjacent; it spawns at the same season; and it occurs at the time of year at which the Bass Strait barracouta would be expected to occur in South Australian waters if they reached that region (Section V(*a*)).

The western group, which starts spawning in April and May, appears to be a different population. The occurrence of near-spawning and spent fish in area XVII in June indicates that the spawning continues into the winter. No information about area XVII is available for the succeeding months. In area XVI, however, spawning and spent barracouta occur in August, and in area IX, the westernmost part of Victoria, similar fish occur in June, July, and August (Section III(*b*)). In area IX these winter spawners are not uncommon and from time to time they support significant fishing operations (catches of about 100,000 lb for the season) throughout the winter; the last good winter of this kind was that of 1942. From what has already been shown of the behaviour and movements of barracouta populations in other waters it may be deduced that the winter spawning fish of areas XVI and IX (eastern South Australia and western Victoria) belong to the same population as the fish which spawn in May and June in the adjacent area XVII (western South Australia); and that this population, which first appears in area XVII in March and April, extends gradually eastward to reach area IX in winter (in greater force in some years than in others), returning probably in spring. The Victorian-South Australian border region is thus occupied alternately by two spawning populations, the Bass Strait population in summer and the South Australian population in winter (Fig. 1); according to fishermen of area IX the winter fish are notably the larger in average size.

Similar information about barracouta captured by research vessels is available for area XIX, the western part of the south coast of Western Australia, and is summarized in Figure 16. Although the species occurs in waters west and north of Albany (to Houtman's Abrolhos, see Section I, Fig. 1) it is apparently very rare in those regions, to judge from the scarcity of reports; most of the reports refer to winter occurrences. It is fairly common from Albany eastwards to Point Culver and has been taken there in May, June, and July, but was not found in March. The area has not been examined by research vessels in other months but several barracouta were taken by a steam trawler in December and January, well off shore and in 75-80 fm, in the western part of the Great Australian Bight (Fig. 16).

In area XVIII, near the South Australian and Western Australian border, only two barracouta have been taken by research vessels, both in May (Figs. 15, 16).

It was shown in Section III(*b*) that the period May-July is a reproductive season for barracouta in area XIX, although nothing is known about the condition of the gonads at other times of year. As the spawning season is broadly the season of greatest availability in surface waters in other regions it is probably the same in Western Australia. Barracouta are probably more plentiful in surface coastal waters in this region in winter than in summer, when they possibly go further off shore, or deeper down, or both.

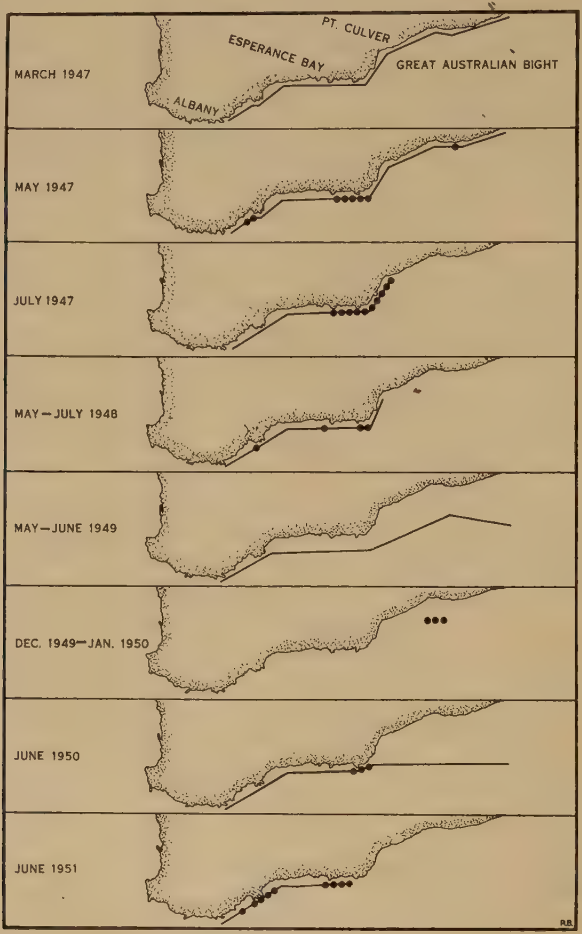
MARCH 1947
PT. CULVER
ESPERANCE BAY
GREAT AUSTRALIAN BIGHT
ALBANY
MAY 1947
JULY 1947
MAY—JULY 1948
MAY—JUNE 1949
DEC. 1949—JAN. 1950
JUNE 1950
JUNE 1951
R.B.

Fig. 16.—Movements of research vessels in southern waters of Western Australia at different periods, showing localities in which barracouta were caught; the sixth panel shows localities in which barracouta were taken by commercial trawling.

Since barracouta spawn in winter in Western Australia and in South Australia and probably in the region of the boundary of the two States (one of the two barracouta caught in May in area XVIII was a ripe male), it is possible that all these fish belong to the same population. But the appearance of the fish in abundance at the same time of year in places as far distant as Western Australia and western Victoria shows that if there is only one population its behaviour is unlike that of any of those described in Section V (*a*). At present it seems more likely that the winter-spawning barracouta of the southern coast of Australia belong to two (or possibly more) quasi-independent populations than that they all belong to one, although there may well be some exchange of individuals between populations.

(*c*) *Comparison with Sea Temperatures*

The fact that barracouta populations north of lat. 38° 30′ S. spawn and are most abundant in surface waters in winter while for those further south the corresponding season is broadly the summer (Sections III(*b*), V(*a*), (*b*)) suggests that the fish prefer waters of a limited range of temperature, at least in the spawning season.

This appears to be true when monthly changes in total catch and catch per boat of barracouta in areas III, XI, and XV are compared with monthly sea surface temperatures contemporaneously recorded in those areas over several years (Rochford 1951 and unpublished data for hydrological stations at Maria I., Port Phillip Heads, and Eden). In area III surface temperatures range from about 13 to 17°C at the times of year at which barracouta are caught and from about 10 to 12° in the winter and early spring, when the fish are absent or very scarce. In area XI temperatures range from about 13 to 19° in the barracouta fishing season and generally fall to 12° in July, August, and September, when the fish are scarce. In the winter of 1950 the recorded temperatures did not fall below 13° and fishing continued all winter (Figs. 12, 13). In area XV, on the other hand, the fishing season is in winter and spring when temperatures range from about 12 to 17°, and fish are scarce or absent in the summer and autumn when temperatures are between 18 and 21°. These observations suggest that barracouta prefer waters between 12 and 19° and specially between 13 and 18°, at least at the spawning season.

At hydrological stations situated successively further north along the coast of New South Wales there is a gradual contraction of the portion of the year at which such temperatures occur (Rochford 1951) and barracouta appear to become correspondingly rarer. At Ulladulla in lat. 35° 22′ S. surface temperatures from 13 to 18° occur during the whole of the winter and spring in some years, but only for 4-5 months in other years; a little barracouta fishing is done in this region in the colder months, possibly much less than the available supply of fish would permit (there is little demand for this species in New South Wales). At Botany Heads in lat. 34° 01′ S. and at nearby Port Hacking the corresponding portion of the year is shorter and at Port Stephens in lat. 32° 43′ S. it is shorter still, averaging only 3-4 months. Although there is no organized barracouta fishing in these latitudes considerable numbers of the fish have been recorded as far north as Port Stephens in the winter and spring months. At hydrological stations still further north (Port Macquarie, Coffs Harbour; see Rochford 1951) surface temperatures hardly ever fall as low as 18° at any time of year; reports of barracouta in these areas (including south Queensland) are few, and refer mainly to the winter.

In other Australian barracouta areas the available temperature data are scanty (Rochford 1951 and other volumes of "Oceanographical station list"; unpublished records in logbooks of research vessels), but observed surface readings at places and in seasons at which the fish are found generally fall within the above-mentioned range. They do so, for instance, in area XIX in winter, in area XVII in autumn, in area XVI in summer, autumn, and winter, and in area IX in winter. Surface temperatures in other parts of Bass Strait differ little from those in area XI and temperatures in other east Tasmanian waters are close to those in area III, and bottom temperatures throughout these regions are generally the same as or lower than the surface temperatures. In the Furneaux Is. (area V), towards which the Bass Strait and eastern Tasmanian populations appear to move as winter approaches, winter temperatures are commonly as high as 13-14° on the easternmost part of the continental shelf at all depths (Section VI). The lowest recorded temperature of water in which large numbers of barracouta were seen in the current investigations was 11° (southern Tasmania); food was very plentiful and the fish were feeding heavily. The highest recorded water temperature near a large concentration of fish was 19° (South Australia).

Thus the movements of the various barracouta populations, as indicated in Sections V(*a*) and V(*b*), appear to permit them to avoid waters which are warmer than 18° or cooler than 13°; although temperatures as high as 19° and as low as 11° are sometimes tolerated.

Similar temperatures prevail in other waters of the world at seasons at which barracouta are plentiful. Hart (1946) stated that the species seems limited to waters where the surface temperatures range from about 10 to about 20°C. He recorded the capture of a specimen off the Patagonian coast in water of 10° (pp. 347, 396). Probably the species can tolerate colder water even than this, as Graham (1939) stated that it is occasionally captured in winter in the Otago region (east coast of South I. of New Zealand), where temperatures at that season are usually about 9° (Sverdrup, Johnson, and Fleming 1942, Chart III). Graham thought that the fish spawn at this season but there is no proof that they do so in the Otago area, and the foregoing observations suggest that that area would then be too cold. If New Zealand barracouta do spawn in winter and spring, as indicated by Thomson (1892), Phillipps (1921), Phillipps and Hodgkinson (1923), and Graham (1939), the spawning is probably confined to the northern part of the region.

VI. The Populations and their Movements

The evidence of heterogeneity of population in the species *Thyrsites atun* in Australian waters may now be reviewed and the information about the different populations summarized. The populations have been recognized by differences in spawning season (Section III), size composition of adult stock (Section IV), and seasonal and annual changes in availability (the former constant and the latter inconstant from year to year; Section V) in different regions. Tagging experiments have furnished little useful information (Section II).

No single one of these pieces of information furnishes indisputable evidence of differences between populations nor does it indicate the full number of populations which exist. Thus differences in spawning season indicate the existence of at least three populations; differences in size composition indicate that one of these three (the group which spawns only in the warmer months) is actually divisible into two; and other considerations (Section V(*b*)) suggest that another of the three (the western group of winter spawners) is also probably divisible. But each piece of information confirms others in part, and taken altogether the mass of information provides very convincing evidence of the existence of different populations as described. The statement which follows is an explanation (and the only explanation which is reasonable in the light of present-day knowledge of the behaviour of pelagic fish populations) of *all* of a very large number of observations of different kinds which have been made, without any preconceived ideas, over many years in most parts of the Australian range of the species.

At least four populations of barracouta, and possibly five or more, occur in Australian waters. The existence of a Bass Strait population, an eastern Tasmanian population, and an eastern Victorian and New South Wales population, can hardly be disputed. In the waters of South Australia and Western Australia there may be one population, two, or a greater number; but it is most likely that there are two populations, which, although their boundaries are unknown, may for the present be called the South Australian and Western Australian populations. Other populations, yet unknown, might exist in the waters of western Tasmania, northern New South Wales, or the west coast of Western Australia.

The bulk of the adult segment of each of the three eastern populations appears to engage each year in a migration and return migration of several hundred miles in all. Six to 9 months of the year are devoted to this movement, and it is during this period that the population renders itself most readily available for capture by man, by passing port after port in spawning or feeding concentrations which make fairly regular appearances at the surface of the sea. Reproduction may occur over most of this migratory period but is much more a feature of the earlier than the later part, i.e. of the outward rather than the inward (return) migration. Feeding occurs over the whole of the period. Waters warmer than 18° or cooler than 13°C are rarely entered. The fish may tend to keep close to land but this is far from certain; they go at least 30 miles off shore and in some areas they seem to approach closer to land on one phase of the migration than on the other. Not all the adult fish necessarily move, or move at the same time or even in the same direction.

Little is known about vertical movement except that it occurs. Barracouta fishermen know that the fish are much easier to find and catch about daybreak (particularly) and sunset than in the intervening daylight hours in most areas; their normal fishing practice is based upon this fact. Presumably this means that the fish migrate to the surface from some unknown distance below it at least once and perhaps twice in 24 hr; once if they remain all night at the surface (as they might in spite of the fact that they are not then caught, because the fishermen rarely fish at night and the barracouta probably would not see the trolled lures if they did), twice if they do not. At times the fish descend to the bottom, even in depths of 100 fathoms; this is indicated by the occasional occurrence of barracouta remains in the stomachs of school sharks (*Galeorhinus australis* (Macleay)) caught by long-lining on such bottoms during the migratory season of the barracouta (Olsen, unpublished data), and by occasional captures in trawl and Danish seine nets and on the hooks of long lines set for sharks.

The exact circumstances of spawning are unknown and running ripe female fish are rarely seen, although males in this condition are commonly found. This probably means that the period of extrusion of eggs is very short (there might, however, be more than one such period per season) and does not coincide with the times of day at which most barracouta are caught. There is nothing to suggest that spawning is confined to certain parts of the region traversed by the population or to certain months of the season of outward migration.

The Bass Strait population appears in early spring at the eastern end of the Strait and moves westward during the spring and summer to the eastern waters of South Australia; it moves back in autumn and disappears towards the eastern waters of Bass Strait in the winter months.

The eastern Tasmanian population appears in late spring on the northern part of the east coast of Tasmania and moves southwards along this coast during the summer and back in autumn, disappearing in winter in the region from which it came.

The eastern Victorian-New South Wales population leaves the Furneaux Is. region in late autumn and moves northward along the east coast of the continent to the southern waters of New South Wales and possibly further north during the winter, returning in spring.

These three populations all appear to begin and end their migrations in the region near the Furneaux Is. (area V). Two of the populations appear to seek this area in winter, the other in summer.

The South Australian population, although not well known, probably engages in similar migrations. It first appears in the western waters of South Australia about mid autumn and seems to move eastward during winter to the western part of the Victorian coast. Nothing is known about return migration but it probably occurs in late winter or spring.

The Western Australian population may behave in a similar way, perhaps moving westward from the Great Australian Bight in winter and back for the summer, but this is largely surmise.

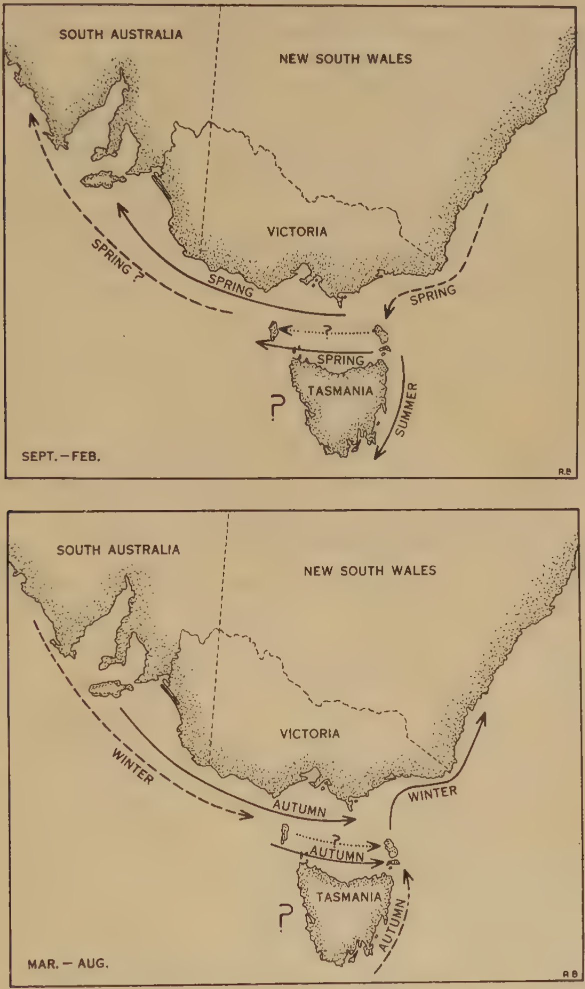
SOUTH AUSTRALIA
NEW SOUTH WALES
VICTORIA
SPRING ?
SPRING
SPRING
?
SPRING
TASMANIA
SUMMER
?
SEPT.—FEB.
RB
SOUTH AUSTRALIA
NEW SOUTH WALES
VICTORIA
WINTER
AUTUMN
WINTER
?
AUTUMN
TASMANIA
AUTUMN
?
MAR. — AUG.
RB

Fig. 17.—Diagrammatic representation of seasonal migrations of the four barracouta populations of south-eastern Australian waters; for further explanation see text.

The movements of the first four of the above-mentioned populations are depicted diagrammatically in Figure 17.

It might be suggested that the three eastern populations, whose geographical ranges all converge upon the neighbourhood of area V, are in reality one population; and that some of its members migrate each year to the north, south, and west, and back in the manner described, spawning at the time of year appropriate to the migratory stream they happen to be in at the time, but with different streams in successive years. Many of the facts which have been observed, but not all, could be explained in this way. The differences in size composition could not be so explained; such differences either would not occur or would occur at random — the fish sometimes larger, sometimes smaller, in one area than in another, according to the vagaries of sampling — which is not the case. In any event this hypothesis would assume that individual fish commonly spawn at intervals of as little as 6 months or as great as 18 months, which is very unlikely and has not been demonstrated for any species of large fish. At most there might be small-scale transfers from population to population in this way, as far as adults are concerned.

Much less is known about the behaviour of these populations at the periods of the year (from 3 to 6 months) when they are not engaged in these migrations, but a good deal can be inferred from the information already presented about the three eastern populations. The fact that the fishermen can no longer catch them might mean that the fish merely go deeper down and not away from the fishing areas at all, but this is most unlikely; their movement in the fishing seasons is unmistakably from and to a certain area, the Furneaux Is. region, where few fishermen operate and where suitable water temperatures, no longer available in the areas of the fishery (even on the bottom), occur in the off season. Undoubtedly there are stragglers which remain in the fishing area in the off season (the winter in Bass Strait and Tasmanian waters, the summer further north), especially on the Victorian side of Bass Strait (Figs. 10-13) ; but it is noteworthy that they were in greater force in that region in the warmer winter of 1950 than in the colder winters of 1949, 1951, and 1952 (Section V(*c*)).

The Furneaux Is. region (area V) is sparsely populated and little fished; the local demand for barracouta is negligible and facilities are poor for sending fish to other markets. The fact that few barracouta are caught therefore does not deny the possibility that they are plentiful. Catches have been made by surface trolling from commercial fishing boats and research vessels at all times of year, but so sporadically that it would be difficult to define optimum seasons.

Conditions in area V and adjacent waters in winter, when it seems that two populations (of Bass Strait and eastern Tasmania) occupy or pass through at least part of the region, are of particular interest. Observations were made in 1950, 1951, and 1953 (and a few in earlier years), and are summarized below.

In waters west of the Furneaux Is. (and in eastern Bass Strait generally) winter sea temperatures are generally 11-12°C and very few barracouta are known to have been caught at that season.

To the east of the Islands, on the inner 10-15 miles of the breadth of the continental shelf (see Fig. 2), the temperatures are also about 11-12°C. More barracouta have been taken here in winter than further west, but still very few, and all by trolling.

Further east still, on the outer 10-15 miles of the shelf which is here 40 to 80 fm deep, temperatures from 13° to 14°C are often recorded at all depths. It was considered that barracouta would probably be more abundant in this warmer area than in any other part of area V and searches were made. Extensive surface trolling operations proved fruitless and it seems certain that barracouta do not visit the surface in this area in winter, at least in the daytime. The only fishing gears which the research vessels could use for subsurface fishing were drift nets, long lines, and deep troll lines, and all were repeatedly employed at different depths without success. A school shark caught in 80 fm had the remains of barracouta in its stomach. A steam trawler which was encountered fishing in 57 fm caught six barracouta which were given to the research vessel. One of them appeared to have been caught while the trawl was being raised, the others probably on or near the bottom (or during the descent of the trawl). Commercial trawlers possibly obtain barracouta quite often in this area in winter, but the point is impossible to prove because they fish other barracouta areas too, and no information about catches in particular areas can be obtained from the trawler owners; and Australia has no research vessel which is capable of efficient trawling.

To the east of the edge of the continental shelf the winter sea temperatures are still generally about 13-14°C in the upper 100 fm of water. Apart from surface trolling, which yielded no fish, little searching has been done in these oceanic waters. The barracouta has never been recorded from oceanic waters and the principal organisms on which they normally feed (the euphausian *Nyctiphanes australis* Sars, and various coastal fishes) are virtually confined to the neritic zone.

The few barracouta trolled by research vessels in the inner shelf waters east of the Furneaux Is., and the above-mentioned six trawled on the outer part of the shelf, were almost all in the condition which would be expected of spring or summer spawning (Bass Strait or eastern Tasmanian) fish in winter. Their gonads were in resting or early filling stages (stages 7, 2, 3, 4) except for a very few males which were further advanced (stages 5 and 6, see Section III(*b*) and Figs. 3, 4). These males were taken in August, close to the Islands, and were probably early-maturing individuals preparing for the spring entry into Bass Strait. It was also noteworthy that most of these fish, particularly the trawled specimens, were plumper and heavier than fish of similar size which are normally taken in the spawning season in Bass Strait or on the Tasmanian east coast.

It thus seems very likely that fish of these two populations (or at least the Bass Strait population) do spend the winter in the Furneaux Is. region or adjacent waters, but the exact location of their main winter quarters is likely to remain unknown until exploratory trawling, preferably with mid-water as well as bottom trawls, can be undertaken. The indications at present are that the fish frequent subsurface neritic waters to the east of the Furneaux Is., and there are grounds for thinking that they would be most abundant over the outer part of the continental shelf in that region. It may be that there are no large concentrations and that the fish are well dispersed over this very large area, seeking food. As yet echo-sounding has thrown no light on the distribution of subsurface barracouta.

The South Australian and Western Australian populations may likewise disappear below the surface when they are not spawning or migrating, possibly to seek particular regions in which to pass the summer. The capture of barracouta by trawling in 75-80 fm in the western part of the Great Australian Bight in summer has been mentioned (Section V(*b*)). In April 1953, on the South Australian coast in long. 136° E. in 46 fm, several barracouta, all except one with pre-spawning gonads and some with benthic crustacea in their stomachs, were taken on long lines set for sharks; up to that time barracouta had not appeared in quantity in any of the adjacent surface waters, although they normally do so about that season, and it is possible that this long-line sample represented the end of a bottom or mid-water phase of life of South Australian barracouta, normally succeeded by a winter pelagic phase.

Little information about the behaviour of barracouta populations is available from other countries. In southern Africa observations have been made and inferences drawn about the annual cycle of the adult fish by Gilchrist (1914, 1916), Heape (1931), Marchand (1935), and Biden 1948). The season at which the barracouta (there called "snoek") is most readily available in the surface coastal waters appears to be successively later, from about early spring through summer and autumn to early winter, in successive localities from about lat. 15° S. on the Atlantic coast to the Cape of Good Hope and thence about 200 miles east (occasionally further) along the coast. They spawn in spring and are then in poor condition ("poor snoek") but during summer and autumn, when the gonads are less active, they become fatter and more valuable to the trade ("fat snoek"). It is not known where they go in winter, and the suggestion by Heape (1931) that "they return to deep water in the southern seas, possibly as far south as the ice cap" and possibly reach Australia in certain years, is pure speculation. It is not even certain that there is only one population in African waters.

On the south-eastern coast of New Zealand (Otago district) Graham (1939) has observed that barracouta occur at the surface from about October to July. At the beginning of this period the fish are thin and appear to have spawned recently; from April to July the gonads develop, nearly but not quite to ripeness, and the fish are in their "best condition" from April to June. They disappear, presumably to spawn, in August and September, and it is not known where they go; a few remain in the same region and Graham is inclined to think that all may do so, but it is more likely that they seek a warmer area (see Section V(*c*)).

At St. Paul and Amsterdam Is. in the South Indian Ocean, the gonads of barracouta ripen about March (Angot 1951).

There are no other useful published observations. Apart from the fact that there are seasonal fluctuations in general bodily condition, probably connected with the annual sexual cycle of the fish (a subject with which it is intended to deal in a later paper on the Australian barracouta), there is little in the results of these overseas researches which closely matches the Australian results or assists in their interpretation.

VII. CONDITION OF THE POPULATIONS

The annual recorded Australian barracouta catch (beheaded and cleaned) averaged about 6,000,000 lb in the decade ending 1939, and probably over several years before that. It fell to about 3,000,000 lb in 1940 and then rose to an unprecedented height, averaging nearly 13,000,000 lb from 1945-46 to 1948-49. In 1949-50 the catch fell to 9,000,000 lb and in the next 2 yr (the latest for which complete records are available) it was back to the pre-war level of about 6,000,000 lb (Table 1, Fig. 18). The Victorian and Tasmanian sets of figures each show a rather similar succession of changes although there are some important differences between them (Table 1).

Blackburn (1950) showed that all these annual variations in the catches up to that time except the decline in 1940 were readily explainable as the outcome of changes in the demand for the fish, which is usually below the catching capacity of the fishermen. Using the total number of fishing boats licensed in each year as a rough measure of fishing effort for barracouta, he also showed that there were no clear signs of any fall in catch per unit of fishing effort on the western part of the Victorian coast, where barracouta fishing has been more intensive and sustained than in any other region of comparable size, since catch records were first kept in 1911. It was therefore concluded that there was no evidence of any depletion of Australian barracouta populations, although the number and extent of the populations were then not known.

It is now possible to dissect the Australian total catch according to populations, for the years since 1947-48 and for two earlier years, 1941-42 and 1942-43 (see Section V(*a*)). Catches in areas I, II, III, and IV have been referred to the eastern Tasmanian population, catches in areas VI, VII, VIII, IX, X, XI, and XII to the Bass Strait population, and catches in areas XIV and XV to the eastern Victorian-New South Wales population. The resulting dissection is shown in Figure 18. The very small catches in areas V and XIII, where two or more populations may occur, have been ignored and the very small winter catches in area IX, which refer to the otherwise unfished South Australian population, have been included with the Bass Strait catches.

Figure 18 shows that the Bass Strait population provides two-thirds or more of the total Australian catch and the eastern Tasmanian population almost all the remainder. The contribution of the third population is insignificant, although it has risen in recent years. The great drop in the Australian catch since 1948-49 is seen to be almost entirely the result of a fall in the catch of the Bass Strait population.

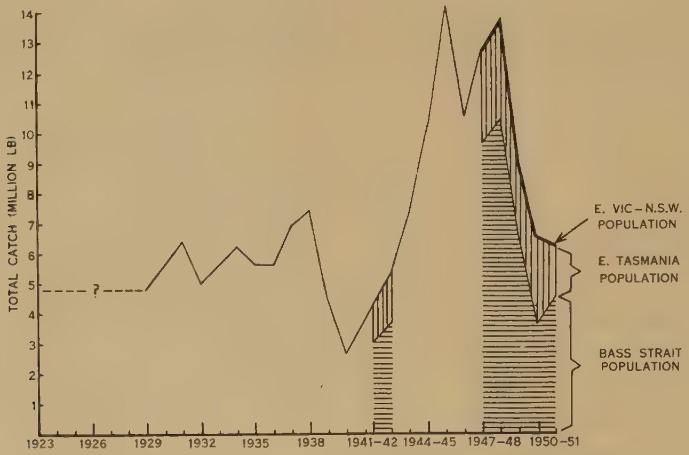

Fig. 18.—Total Australian annual barracouta catches (beheaded and cleaned) and their dissection according to populations.

Figures 12, 13, and 14 show that although total catches for Bass Strait areas began to fall in 1949-50 the area catches per boat-month did not fall appreciably until the following year. That is to say, the fall in total catch of Bass Strait fish from 10,400,000 lb in 1948-49 to 6,600,000 lb in 1949-50 was not the result of a decline in the availability of fish; it was the fishing effort which declined, reflecting the lower demand. The export market for canned barracouta was lost about this time, and local sales of canned, smoked, and fresh barracouta declined as a result of the greater availability of competing Australian and imported fish of other species. But the subsequent decline in total catch, which was only 3,600,000 lb in 1950-51 and 4,500,000 lb in 1951-52, was certainly due to scarcity of barracouta in the fishing areas; the fish were actually scarcer to the catchers and complaints of gluts were succeeded by complaints of shortages.

The cause of this scarcity is not known but some possible causes can probably be eliminated. One could suspect depletion of the population (the result of overfishing), adverse natural fluctuation in abundance of the entire population, or adverse natural fluctuation in availability of the population to the fishermen, i.e. a change in behaviour of the fish.

Depletion seems very unlikely. The fishery has every appearance of one of low intensity (Blackburn 1950; and Section II of this paper, on tagging). The average size of fish was lower in 1951-52 and 1952-53 than in 1945-46 but this was the result of heavy fishing of small fish (of which, incidentally, there appears to be no present shortage) after the early disappearance of those of normal size; there was no obvious change in the proportion of large to medium-sized fish (Section IV, Figs. 6-9). Neither a hypothesis of depletion nor one of natural fluctuation in abundance of the whole population can be reconciled with the fact that the scarcities of 1950-51 and 1951-52 manifested themselves in the autumn only; the spring fisheries of those years, operating on the same population, encountered fish in normal (1950-51) or greater than normal (1951-52) numbers. Another significant point is that one part of Bass Strait, area XII, did not suffer from unusual scarcity in either autumn.

One is left with natural fluctuation in availability of the population as the most probable explanation of events in these two autumns. That is to say, the behaviour of the population was unusual in those two seasons; the weather, with regard to its possible effect on fishing operations, was not. It is unlikely that the fish were present as usual and merely not biting, or fishermen would have remarked on it. The data of Figures 8, 12, and 13 indicate that in 1951-52 most of the adult fish had finally left the fishing areas before May (normally a good fishing month) or even earlier; this shortening of the season might be a sufficient explanation of the low catch of that autumn but it could hardly explain that of the previous autumn when the season was not so much short as bad throughout. It is possible that the fish followed an unusual migratory path in one or both of those seasons, appearing near the coast in their normal numbers only in area XII; or that they remained to an unusual extent below the surface except in area XII; and that, at least in 1951-52, the autumn (return) migration was also unusually early. Hydrological and planktological investigations have been undertaken in the hope of reconstructing and explaining the events that took place, but the work is only in the early stages.

The current period of comparative scarcity of barracouta in the fishing areas of Bass Strait is not the first that has occurred in the region. Catches were also low in most fishing areas on the Victorian side of the Strait about 1940 and 1941 (Table 1, see Blackburn 1950 for further details) in spite of good demand and normal fishing effort. They were possibly low on the Tasmanian side also, to judge from the very low total Tasmanian catch of 1940 (Table 1). Old fishermen on the north coast of Tasmania speak of a more distant time (not identifiable) when barracouta were altogether absent from that region. It may be normal for two or three successive bad years to occur from time to time in Bass Strait.

Catches of barracouta of the eastern Tasmanian population were fairly constant at from 2,000,000 to 3,000,000 lb annually from 1947-48 to 1950-51, but only about 1,600,000 lb were taken in 1951-52 (Figs. 12, 18). The area catches per boat-month also fell in 1951-52, but not earlier (Fig. 13). The lower catch of that year therefore does not signify any fall in demand, and it is even less likely to signify depletion than the above-mentioned fall in the Bass Strait catch; there is less fishing in eastern Tasmania than in Bass Strait, and the fish are larger. A natural fluctuation in the size of the whole population (i.e. in abundance) or in the size of the part of the population within reach of the fishery (i.e. in availability) must be presumed, and it is noteworthy that the fluctuations in this and the Bass Strait populations do not altogether coincide; 1950-51 was a bad year for barracouta in Bass Strait and a normal one in eastern Tasmania, and 1951-52 was bad in both regions.*

The cause of this fluctuation is not known and nothing is known with certainty about previous fluctuations in the eastern Tasmanian population. Catches in 1941-42 and 1942-43 were only about 1,300,000 and 1,600,000 lb respectively (Fig. 18, data from Blackburn 1950) but this was probably an effect of demand (Blackburn 1950).

Little can be said about the condition of the other populations except that they are obviously under-fished, indeed virtually unfished. The relatively good fishing obtained in area XIV in the winter of 1951 probably represents a favourable natural fluctuation of some kind in the eastern Victorian-New South Wales population (Section V(*a*)). An interesting fluctuation has occurred in the winter fish of area IX, which were fairly plentiful in several winters ending with that of 1942 but have since been much scarcer (Section V(*b*), see also Figs. 10, 11). Again the cause of the change is unknown but the change itself is not remarkable; the occurrence of these fish represents the easternmost extension of the otherwise unfished South Australian population in its migratory phase, and the distribution of individuals at the extremes of the range of an animal population is often markedly inconstant.

Although not depleted and probably not even well fished, the Bass Strait and eastern Tasmanian populations may have been altered to some extent by fishing operations; this could explain why fish over 90 cm L.C.F., for example, are less common in Bass Strait than in the more lightly fished waters of eastern Tasmania (Section IV) and probably less common in the latter region than they once were (Blackburn 1950). As barracouta often eat the young of their own species a reduction of numbers of large fish in a population is probably beneficial to the population as a whole.

It has been shown that the Bass Strait and eastern Tasmanian populations can yield (between them) 13,000,000 lb annually when natural fluctuations are not adverse, without being overfished. This is twice the amount they yield at present and have generally yielded in the past. But as recaptures of tagged fish have never exceeded 1 per cent. of the number released (Section II) and as the populations are only fished during 6-9 months of each year and then only in certain small areas (within a few miles radius of each of a few ports in the total area of each population) and with primitive fishing gear, it is almost certain that these two populations could safely yield a great deal more than 13,000,000 lb, probably many times that amount. And when it is considered that there are at least two and probably three other populations (of eastern Victoria-New South Wales, South Australia, and Western Australia), which are all apparently of considerable size and yet virtually unfished, it seems reasonable to believe that a catch about 10 times as great as the present Australian barracouta catch could be taken if all the available populations were adequately exploited, without overfishing any of them, if the demand required it.

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* 1952-53 was bad in Bass Strait and normal in eastern Tasmania; see footnotes in Section V(*a*).

Such an annual catch, say 63,000,000 lb of beheaded and cleaned fish, would be equivalent to about 90,000,000 lb of fish in the round. The present (1951-52) total Australian commercial catch of aquatic animals in the round (excluding whales, and molluscs in the shell) is also about 90,000,000 lb (Kearns 1953, Table) ; it could probably be nearly doubled from barracouta populations alone.

Any increase in the utilization of the three virtually unfished populations would have the effect of making fresh barracouta available to consumers all the year round, if it were properly distributed; a plentiful supply of winter fish, which at present cannot be obtained from the other populations, would be readily available. And the effect of adverse natural fluctuations upon the total catch would probably be less marked than it is at present, because the several populations would probably never all fluctuate alike.

However, the present total demand for Australian barracouta is probably only about 50 per cent. higher than the pre-war demand. The pre-war catch was about 6,000,000 lb (beheaded and cleaned) with demand fully satisfied; the catch of 1949-50 was about 9,000,000 lb with demand fully satisfied; and the catch of each of the two following years was about 6,000,000 lb with demand unsatisfied.

VIII. CONCLUSIONS

(1) There are at least three populations of barracouta in the coastal waters of south-eastern Australia: one which visits Bass Strait and its western approaches in the spring, summer, and autumn; another which visits eastern Tasmanian waters in summer and autumn; and a third which visits the waters of eastern Victoria and southern New South Wales in winter and spring.

(2) These visitations consist of migrations — west through Bass Strait, south along the east Tasmanian coast, and north along the east Victorian and New South Wales coasts, respectively — and opposite return migrations east, north, and south, by the bulk of the adult members of the populations. The populations are fished while they are making these migrations.

(3) The adults of each population spawn during the migratory period, especially in the initial period of outward migration. Thus the Bass Strait and eastern Tasmanian populations consist mainly of spring or summer spawners while the eastern Victorian-New South Wales population consists mainly of winter or spring spawners. Very few fish under 50 cm (length to caudal fork), but most of those over 60 cm, and almost all over 80 cm, are sexually mature.

(4) Each population feeds while migrating, even during the spawning period.

(5) During these migrations the barracouta are usually found in water of temperatures between 13 and 18°C. When the waters become cooler (Bass Strait and eastern Tasmania in winter) or warmer (New South Wales in summer) most of the fish vacate them altogether; they then appear to seek an area near the Furneaux Group at the eastern approach to Bass Strait, where conditions are more suitable at those seasons.

(6) In the coastal waters of South Australia and southern Western Australia there are probably two large barracouta populations, one in each State; both spawn in late autumn and winter. The South Australian population probably migrates from western South Australia to western Victoria during the spawning season. The Western Australian population may also make migrations.

(7) Elsewhere in Australian waters, except possibly in western Tasmania which has been little investigated, the barracouta is scarce or absent; its northernmost extension is to about lat. 28°S. on both the east and west coasts of the continent.

(8) About two-thirds of the Australian catch is normally taken from the Bass Strait population and most of the remainder from the eastern Tasmanian population; the other populations are unfished or very little fished. The total catch of cleaned and beheaded fish rose from about 6,000,000 lb before the war to about 13,000,000 lb in the first 4 post-war years, in response to an unusually great demand; it then fell to about 6,000,000 lb in 1950-51 and 1951-52.

(9) The fall in the Australian catch after 1948-49 was mainly the result of a fall in the catch of the Bass Strait population; it began as a decline in demand in 1949-50 and continued in 1950-51 and 1951-52 as a decline in actual availability (catch per unit fishing effort) of the fish of that population. The fish were scarce on the return (autumn) migrations only, being in normal or better-than-normal numbers on the outward

(spring) migrations of the same years: it is therefore considered that the scarcity was due to change in population behaviour, rather than in population size.

(10) Over the same period the availability of fish of the eastern Tasmanian population was fairly constant until 1951-52, when it fell.

(11) No population exhibits any symptoms of depletion; the fisheries have the appearance of being of low intensity, and only seven tags were recovered out of a total of 4600 released over a period of 5 yr.

(12) It is probable that the combined barracouta populations could yield an annual catch of 10 times the present size without causing any depletion; this would almost double the total Australian catch of fish and crustaceans.

IX. Acknowledgments

Much of this paper is based on observations and experiments made at sea from the C.S.I.R.O. Fisheries Research Vessels *Liawenee* (1948-1950) and *Derwent Hunter* (1950-53) under the command of Captain R. Downie. The authors are greatly indebted to Captain Downie and the members of his crews for much painstaking assistance and welcome initiative and advice. Their thanks are also due to Messrs. J. C. Dowsett, W. J. Fletcher, and W. G. Scott of the Division of Fisheries, C.S.I.R.O., for technical assistance on the vessels and in the fishing ports.

Much use has been made of data collected earlier by Mr. J. A. Tubb, formerly of the Division of Fisheries, and other earlier observations made from the Fisheries Research Vessel *Warreen* under the command of Captain A. Flett and Captain C. E. Pedersen. Dr. J. M. Marchand, Director of Fisheries in the Union of South Africa, kindly gave permission to mention unpublished tagging results obtained by him in that country.

Many other people have helped. Among them must be mentioned Mr. M. D. Barker of Ulverstone, Tas., for the measurement data of Figure 7; Miss H. N. Turner, of the Section of Mathematical Statistics, C.S.I.R.O., for the regression equation of Section I; and Miss B. McGrath and Mr. R. Breach, of the Division of Fisheries, C.S.I.R.O., the former for compilation of data and the latter for preparation of figures.

Finally, thanks are due to the Director and officers of the Department of Fisheries and Game, Victoria, and the Secretary and officers of the Fisheries Division, Department of Agriculture, Tasmania, for keeping and making available valuable statistical records of the barracouta fisheries.

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THE ORGANS OF FEEDING AND THE FOOD OF SOME AUSTRALIAN MULLET

By J. M. THOMSON*

(*Manuscript received January* 15, 1954)

Summary

The morphology of the jaws of six species of mullet (Mugilidae) is compared and illustrated. The maxilla is not fused to the skull and in two of the species the upper end moves forward during protrusion of the mouth. The premaxillae are protruded by the thrust from the internal hook of the maxillae. Three adductor and two protractor muscles attach to the maxillae. Their origins and insertions and mode of action are described. The disposition of minute teeth on the lips, tongue, and bones of the palate and on the pharyngeal pads is detailed. Counts of gill-rakers, pyloric caecae, and mucous ridges in the stomach are given. The gut contents of each species as revealed in intermittent observations are tabulated and compared with reports from elsewhere. In general mullet feed on any small organic material wherever it occurs in quantity, but the amount of crustacean or mollusc material is small except in individuals with the best-developed teeth.

I. INTRODUCTION

The recent revision of mullet genera by Schultz (1946) focused attention upon the fact that evolutionary variation in this anatomically uniform group has been confined largely to the mouth-parts. In this paper a number of intermittent observations on the stomach contents of various species of mullet is presented. As further work is unlikely an attempt is made to correlate the type of food-stuff with the development of teeth and the extent of jaw protrusion. The jaw musculature and its mechanism are described in some detail as previous descriptions omit mention of some of the muscles involved.

II. THE JAWS AND THEIR MUSCLES

The mouth is terminal in the majority of mullet and is so in all known Australian species.

(*a*) *The Upper Jaw*

In the Mugilidae the upper jaw is formed by the premaxillae, the maxillae being excluded from the gape. Kesteven (1926) has suggested that these should be termed the premaxillary labials and maxillary labials respectively, as they are not truly homologous with the premaxillae and maxillae of tetrapods. Kesteven maintained that the bones usually called vomers and palatines are the true homologues of tetrapod premaxillae and maxillae. However, the more normally adopted terminology will be used here.

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* Division of Fisheries, C.S.I.R.O., Cronulla, N.S.W.

When the mouth is closed the maxillae lie parallel to and behind the premaxillae and usually are hidden beneath the preorbitals for all or most of their length. The maxillae meet the premaxillae in a movable joint at the corner of the mouth gape just inside the coronoid process of the lower jaw. Both bones are somewhat expanded towards the joint — the premaxillae more so than the maxillae. An exception is *Aldrichetta forsteri* (Valenciennes), where the premaxillae narrow at the joint after an intermediate flaring (Fig. 1*E*). In some genera this lower part of the

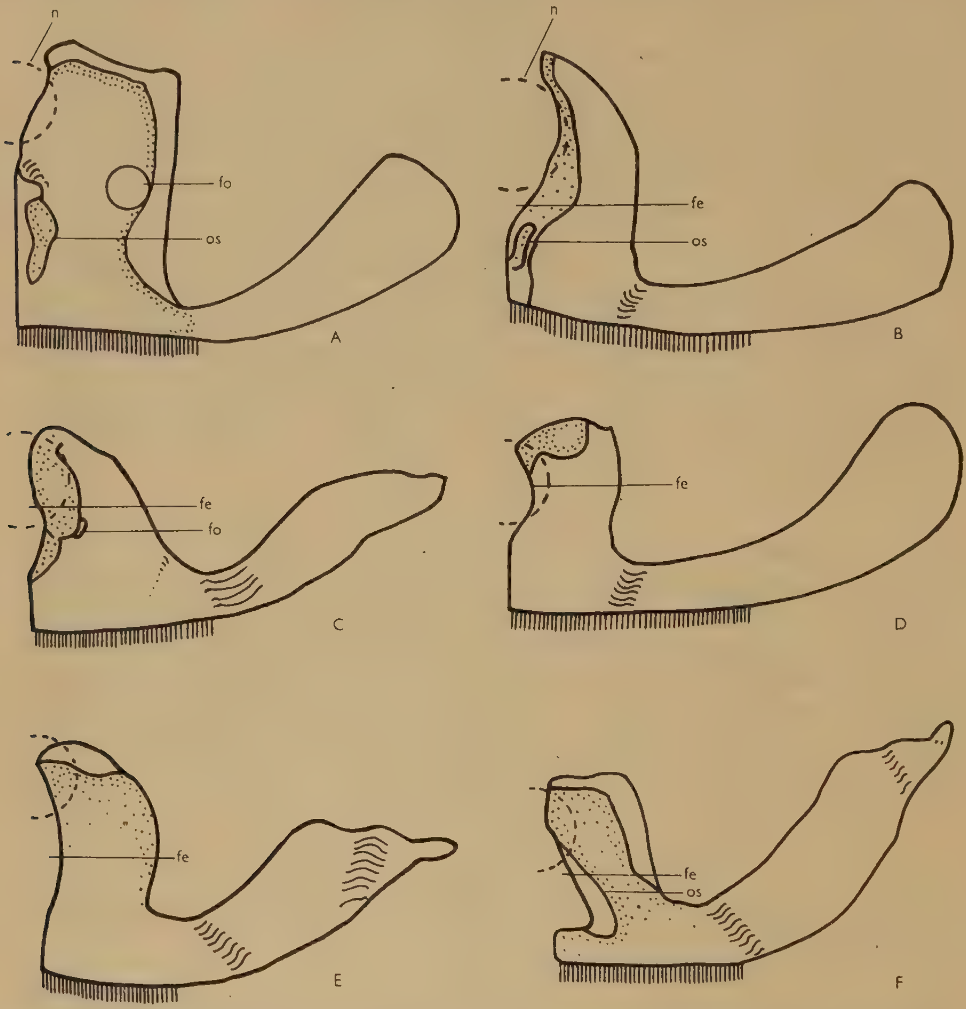


Fig. 1.—Premaxillae: left lower surface (the right premaxilla is the mirror image of the left). The dotted line indicates the position of the ball of gristle. *Fe*, fenestrum, *fo*, foramen; *n*, notch; *os*, ossicle. In all figures, except Figure 5, the species are indicated by (*A*) *Mugil cephalus;* (*B*) *Mugil georgii;* (*C*) *Liza argentea;* (*D*) *Liza dussumieri;* (*E*) *Aldrichetta forsteri;* (*F*) *Myxus elongatus.*

jaws continues in the main axis of the bones; but in others it bends sharply downwards (Fig. 1).

Medianly the premaxillae bear posterior expansions which are more or less fused in the median line. When the jaw is retracted these fit under the dorsal skin of the skull in the space left between the ethmoid bones. The exact shape of the posterior expansion varies. Usually it is more or less rectangular in outline, but is somewhat rounded in *Liza argentea* Gunther. In most species there is a foramen in each expansion — but this is absent in *Myxus elongatus* Gunther. The median fusion is not complete. Usually there is a central space, the *fenestrum,* between the two expansions, while the fusion is complete posteriorly. But in *Mugil cephalus* Linnaeus there is only a posterior notch and no fenestrum. Ventrally each expansion has a raised ossicle towards the anterior end. These ossicles are absent in *Liza argentea.* The posterior portion of the expansion is concave beneath and in this rests a ball of gristle. This covers the notch in *M. cephalus,* indicating that the notch is not homologous with the fenestrum, as the gristle ball barely reaches the fenestrum in other species and in those species with a fenestrum the ossicles border it; whereas the ossicles are anterior to the notch in *M. cephalus.*

Each maxilla is a slender bone of somewhat twisted appearance, bearing at the upper end a ball joint beneath which is the so-called internal hook whose distal end is bound tightly to the ossicle of the premaxillar expansion on its side. Tissue also connects the hook to the ball of gristle beneath the expansion. Various ridges can be distinguished upon the maxillae where muscles attach. Details vary in each species (Fig. 2). In *Aldrichetta forsteri* there is a marked groove on the outer face of the maxilla.

The maxilla itself is not fused with the skull and takes a varying part in the protrusion of the mouth. The lower portion generally moves forward somewhat and becomes visible behind and below the premaxilla; but in four of the six species investigated (belonging to the genera *Liza, Myxus,* and *Aldrichetta*) the upper portion of the maxilla does not move outwards but appears to rotate on the point of a narrow prolongation of the palatines, just under the preorbital. However, in the two species of *Mugil* this upper portion also moves forward. In *Mugil cephalus* the movement is slight — barely as far as the maxilla's own breadth — and is more apparent in larger specimens. But in *Mugil georgii* Ogilby the upper end of the maxilla moves out to a position half way between the premaxillae and the skull proper.

Usually the maxilla is held in place by connective tissue which binds the upper end to the preorbital and the ethmoids, but in *M. georgii* this has not occurred and the maxilla moves out to the limit permitted by the large ligament which anchors the ball joint of the maxilla to the palato-vomerine fusion. This ligament is smaller in *georgii* and correspondingly the ball joint of the maxilla is large and rounded. In other species where

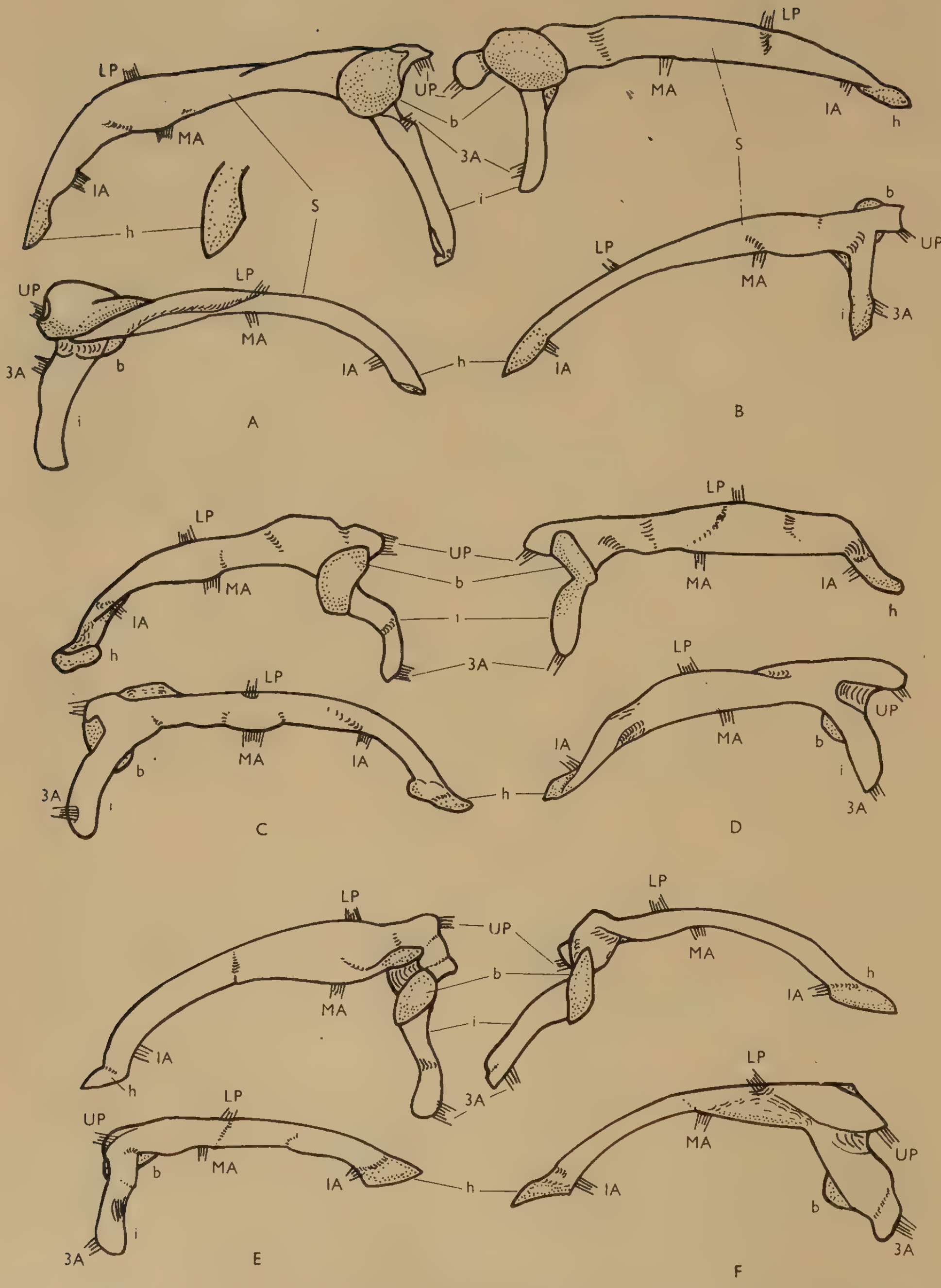


Fig. 2.—Maxillae: lower surface above; upper surface below; lines radiating from the bone indicate muscle attachments. *b*, Ball joint; *g*, groove; *h*, heel; *i*, internal hook; *s*, shaft; 1*A*, minor adductor; *MA*, major adductor; 3*A*, third adductor; *LP*, lower protractor; *UP*, upper protractor.

the ligament is less well developed the ball joint is small and narrow (Fig. 2).

The internal hook of the maxilla is better developed in species where the upper end of the maxilla is bound to the skull, as the protraction depends entirely on the thrust of the hook on the premaxillae.

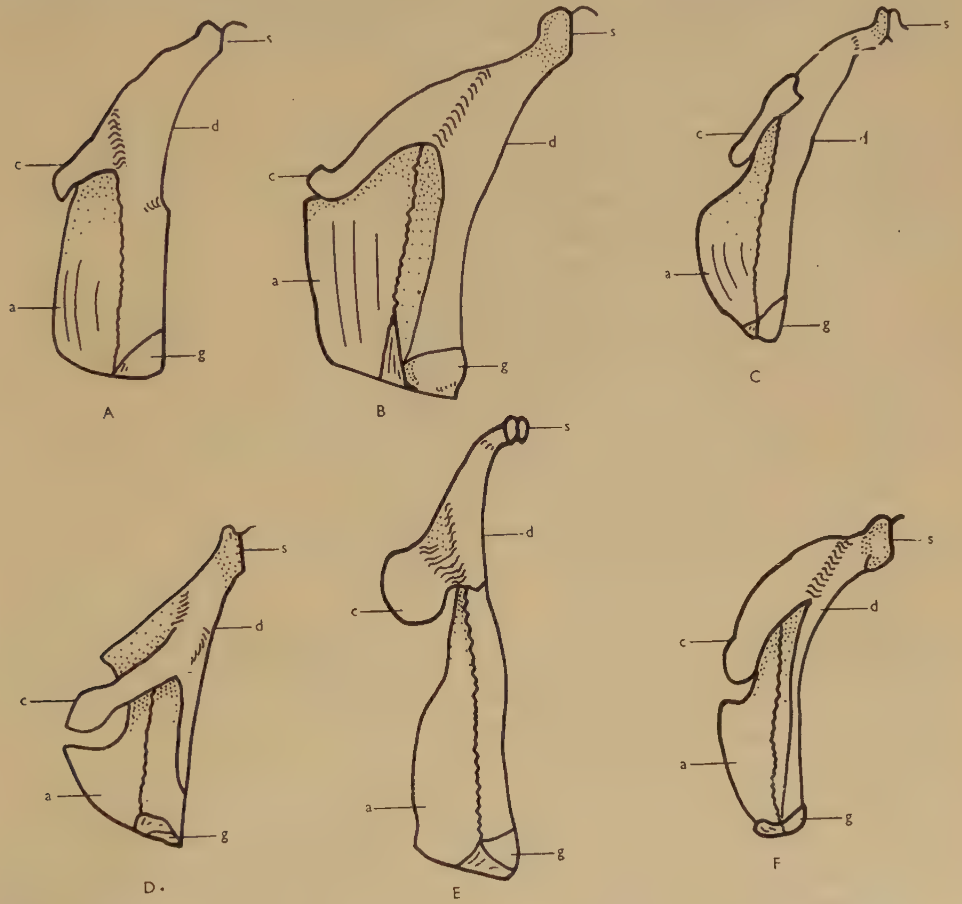


Fig. 3.—Mandibles; upper (inner) surfaces. *a*, Articular; *c*, coronoid process; *d*, dentary; *g*, angular; *s*, symphysis.

(*b*) *The Lower Jaw*

The lower jaw consists on each side of a posterior articular tipped by a small angular and an anterior dentary which bears the coronoid process posteriorly. Medianly the dentaries fuse into a symphysis which is marked by a symphysial knob which appears more or less double, being rather concave medianly on the dorsal side. Haines (1937) claimed that the bone usually called the articular is the true angular and the so-called angular is the retro-articular, but the more generally accepted terms will be used here.

In *Liza dussumieri* and *Mugil georgii* the jaw-line is almost straight from symphysis to coronoid process, but in the other four species it curves gently backwards, more so in *Mugil cephalus, Aldrichetta forsteri,* and *Myxus elongatus* than in *Liza argentea* (Fig. 3).

The articular works against the quadrate where it lies behind the pterygoid. The quadrate in turn works on the skull via a narrow symplectic, a metapterygoid, and the hyomandibular.

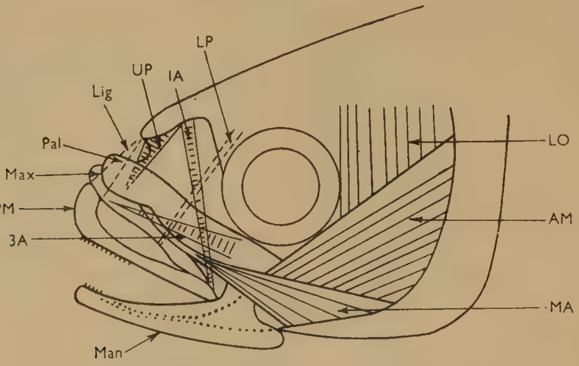


Fig. 4.—Diagrammatic representation of the course of the jaw muscles of a mullet.

(c) *The Myology of the Jaws*

The course of the muscles is shown diagrammatically in Figure 4.

(i) *The Upper Jaw.*—There are five muscles attaching to each maxilla plus the large ligament from the palato-vomerine fusion anchoring the ball joint of the maxilla. Two of these muscles may be termed protractors or levators. One, the upper protractor maxillae, is inserted on the head of the maxilla external to the ball joint. Its origin appears to be on the ethmoid and nasals as a thin sheet of muscle which becomes concentrated in the region of the nostrils where it lies close to the integument. The lower protractor maxillae is inserted on the outer edge of the shaft where the maxilla attains its greatest curvature, about one-third of the distance from the corner of the mouth. The insertion is on a definite shoulder or ridge which breaks the symmetry of the curve of the maxilla. The origin of the lower protractor maxillae is on the sphenotic.

The major adductor maxillae is inserted opposite the lower protractor maxillae on a slight bulge of bone. This is the muscle identified by Eaton (1935) as the *A*1 or lower external adductor of Vetter (1878). However, Kesteven (1943) termed this the tempero-massetericus. The term major adductor will be used here as describing best its function. It arises as a small flat sheet of muscle from the inferior edge of the quadrate and the adjacent lower edge of the preopercular. It passes into a tendon at the level of the anterior edge of the eye and this tendon inserts on the maxilla as described.

A minor adductor maxillae is inserted on the maxilla about half way between the insertion of the major adductor and the "heel" of the maxilla, it passes obliquely upwards, running externally to the major adductor, and inserts under the ethmoid.

The third adductor is inserted on the shaft of the internal hook of the maxilla on a ridge running down part of its length and running under the maxilla it arises under the preorbital.

(ii) *The Lower Jaw.*—There is a massive muscle originating on the outer edge of the quadrate, symplectic, and hyomandibular; it passes into a tendon which is inserted on the inner face of the articular bone of the lower jaw behind Meckel's fossa. This is here termed the adductor mandibulae as descriptive of its function. However, according to Kesteven (1943) the *A*2 is absent or fused with the *A*1 (the major adductor maxillae) and Eaton's *A*2 was regarded as the pterygoideus by Kesteven.

The supplementary adductor mandibulae — probably homologous with the *A*3 of Vetter, originates on the face of the metapterygoid and inserts on the inner surface of the tendon of the adductor mandibulae. The protractor hyoideus (geniohyoideus of Al-Hussaini (1949)) is a flattened muscle originating on the lateral surfaces of the ceratohyal and the hypohyal; it is inserted on the mandibles just to one side of the symphysis. The muscles of the two sides are practically continuous medianly. A peculiar feature is that near the insertion on the mandible a few fibres pass through the overlying submentalis muscle so as to insert dorsally on the dentary.

Also concerned in the action of the lower jaw is the levator arcus palatini which arises from the post-orbital process of the sphenotic and passes to the head of the hyomandibular.

(*d*) *Functioning of the Jaws*

The protractor hyoideus pulls on the tip of the lower jaw so as to open it, simultaneously the maxilla is rotated along its long axis by the action of the upper and lower protractor maxillae pulling so that the outer surface of the maxilla revolves dorsally; thus sending the internal hook rotating downwards and forwards. As the internal hook is tightly bound to the premaxillar expansion the premaxilla is thrust forward.

In closing, the pterygoideus pulls the lower jaw to the horizontal position and the three adductors rotate the maxilla so that the internal hook rolls downward and backward, taking the premaxillar expansion to its resting position between the ethmoids.

Meanwhile the leveator arcus palatini, the stenohyoidei muscles in the tongue, and the dilator operculi with the muscle of the branchial arches create a sucking action by which food material and water (together with other matter) are taken into the mouth.

Plate 1 illustrates the mouth closed and Plate 2 the mouth open, in two species of mullet, *Liza argentea* and *Mugil cephalus*. In the genus *Liza* the lower end of the maxilla is visible as a dark patch in front of the preorbital. In the other genera the lower end fits into a recess under the preorbital. In the illustrations with the mouth open (Plate 2) it can be seen that the upper end of the premaxilla (lining the upper lip) diverges from the maxilla, which runs from the corner of the mouth up under the upper end of the preorbital. The mandibular symphysis is clearly apparent in *Liza argentea* (Plate 2, upper).

III. The Buccal Cavity

The aperture of the mouth is roughly the shape of a chevron in the species examined except in *Aldrichetta forsteri* and *Myxus elongatus*, which are more gently rounded and elongate laterally, with a lunate cross section.

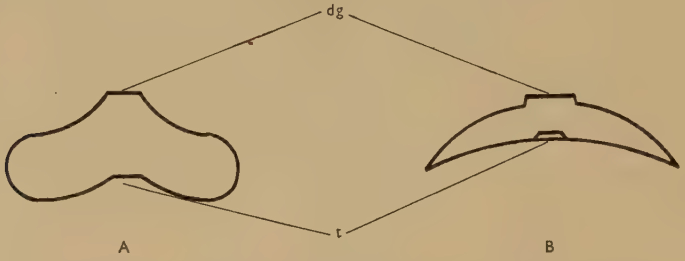


Fig. 5.—Cross section of mouth of (*A*) *Mugil georgii*; (*B*) *Myxus elongatus*. *dg*, dorsal groove; *t*, tongue.

The general shape continues in the dorsoventral cross section of the mouth — the central bump of the symphysial knob being continued in a low ridge of tissue which ends at the tongue which itself raises the floor of the mouth. In *Liza dussumieri* particularly the tongue is ridged dorsally, but the ridging is lower in the other species, and absent entirely in *Myxus elongatus* (Fig. 5).

The disposition of the teeth on the lips and other mouth-parts is shown in Table 1. The teeth on the lips are not inset in sockets of the jaws but merely set upon the jaw bones basally. With age they tend to become fewer in number (e.g. in *Mugil cephalus* and *Aldrichetta forsteri*) or to become embedded in the lip (*Liza dussumieri, L. argentea*).

The arrangement of the gill arches has been described by Al-Hussaini (1947) for *Mugil auratus* Risso. All the Australian species are similar except in the number of gill rakers (Table 1). The posterior rakers of the last arch are modified to form a concave floor on each side of the mouth separated from each other by a ridge formed by the pharyngeal membrane. These modified rakers are prolonged and fused laterally so no water can pass between them.

Corresponding to these concavities are the convexities of the two dorsal pharyngeal pads which project in a bulge from the roof of the mouth. These pharyngeal pads are highly papillate and in some species are studded with minute teeth. Ghazzawi (1935) has recorded such teeth for *Mugil capito;* but Al-Hussaini (1947) said these are not present in *M. auratus.* Such teeth are present in all the Australian species studied. They become more numerous (or at least more apparent) with age. They are most dense in the anterior edge and centrally. In *Liza argentea* they are confined to two areas, only papillae occurring laterally and posteriorly. In large specimens of *Aldrichetta forsteri* the entire pad is studded with teeth, but in the young the distribution is similar to that of *Liza argentea.* All the pharyngeal teeth are simply pointed, though often they are in such dense patches they seem at first glance to be multi-cusped. However, the shape differs in each species (Fig. 6). The expanded basal portions are embedded beneath the surface membranes of the pads.

TABLE 1

ARRANGEMENT OF TEETH AND NUMBERS OF PRIMARY GILL RAKERS AND OF PYLORIC CAECAE

	Mugil cephalus	*Mugil georgii*	*Liza argentea*	*Liza dussumieri*	*Aldrichetta forsteri*	*Myxus elongatus*
Teeth in upper jaw	X	X	X	X	X	X
Teeth in lower jaw	X	X	X	X	X	X
Teeth on vomers	O	O	X	X	X	X
Teeth on palatines	O	O	X	X	X	X
Teeth on pterygoids	O	O	X	X	X	O
Teeth on tongue	O	O	X	X	X	O
Teeth on pharyngeal pads	X	X	X	X	X	X
Gill rakers	$\frac{24\text{-}36}{50\text{-}76}$	$\frac{20}{56}$	$\frac{42}{100}$	$\frac{28}{68}$	$\frac{19^{*}}{34}$	$\frac{24}{40}$
Pyloric caecae	2	22	2	5	2	2
Ridges in stomach	16	10	14	14	8	9

* Young specimen. X Present. O Absent.

A fold of tissue from the posterior edge of the upper and lower pharyngeals forms a kind of valve, so that the mouth does not end in a round orifice but in a slit which almost reduplicates the chevron or lunate section of the mouth. The slit dilates to permit passage of food.

The buccal cavity is lined by a stratified epithelium with abundant taste-buds and mucous cells. The solid matter contained in the water is strained by the gill rakers. Material of suitable size passes to the oesophagus by muscular contraction — presumably only when the taste-buds advise that food is present. Otherwise the sand or mud particles are ejected from the mouth. This characteristic spitting reaction which may be clearly seen in an aquarium and in fish feeding on shallow banks, reveals the presence of mullet to the fishermen who describe the muddy patches produced as "mullet water".

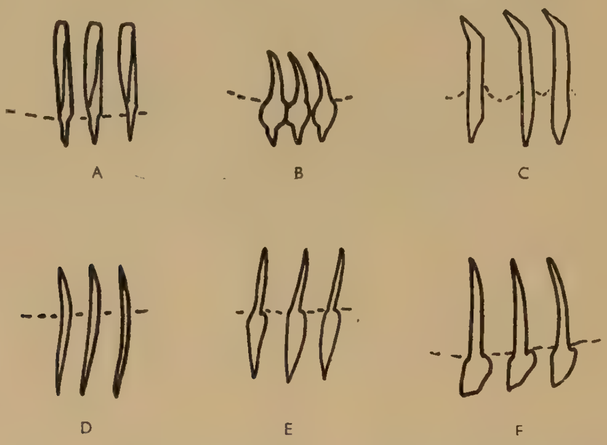


Fig. 6.—Teeth of the pharyngeal pads. Dotted line indicates the surface of the pads, free portion above dotted line, embedded portion below.

IV. The Intestinal Tract

The oesophagus is a straight tubular portion of the gut whose internal surface is smooth at the buccal end but becomes complexly folded near the stomach. According to Al-Hussaini (1949) this change is accompanied histologically by a change from stratified epithelium with saccular mucous cells to a columnar epithelium with goblet-shaped mucous cells.

The oesophagus opens about half way along the stomach length, its cavity being separated from that of the stomach by a valve formed from the mucous folds. These are continuous via the valve with the folds of the internal membrane of the stomach. The number of folds varies from species to species (Table 1).

The stomach is divided into two sections. Externally the stomach is globular at the anterior end with a median ridge encircling it and at the posterior end is a saccular portion which is flaccid if no food material is contained. Internally the posterior end, which is a blind caecum, is saccular and thin-walled. The anterior portion is a thick-muscled gizzard-like structure whose cavity is reduced to a mere slit. Its function is to triturate the food. Ishida (1935) described the inner lining of this portion as horny; but Ghazzawi (1935) and Al-Hussaini (1947) asserted that it is a thick mucous plate and such seems to be the case.

At the anterior end of the gizzard a pyloric valve guards the opening to the intestine. In this region the pyloric caecae open. These, according to Babak (1903), are sources of diastase and trypsin-like enzymes. What may be the exact significance of the number of pyloric caecae is unknown. Most species have only two (Table 1) ; but *Mugil georgii* has 22; of which only 14 are visible when the body cavity is cut open; the remainder being obscured under the lobes of the liver.

The intestine is thin-walled and of considerable length. The relative gut length as determined according to the method of Al-Hussaini (1947) is almost identical for all the species, namely from 5.5 to 5.7, which differs from Al-Hussaini's figure of 3.7 for *Mugil auratus*. It is thrown into a number of loops, there being five bends or 2½ loops — considerably fewer than the 20 quoted by Cuvier and Valenciennes (1827). The intestine appears in section to be lined by a columnar epithelium which Al-Hussaini (1947) says are actually curved cells and not strictly columnar. In the rectal region the submucosa is highly vascular.

V. The Food

The food of Australian mullet as revealed by intermittent observations is shown in Table 2. The number of observations is not large but some tentative conclusions are justified.

Referring from Table 2 to Table 1 it will be seen that the species which secure the most active crustaceans or larger-sized material such as molluscs are those which are better equipped with teeth.

An interesting comparison between similar-sized mullet of different species feeding on the same bank is afforded by samples (8) of *Mugil cephalus* and (2) of *Aldrichetta forsteri*. These fish were netted together; besides the sand, detritus, and diatoms which specimens of *Mugil cephalus* contained, specimens of *Aldrichetta forsteri* also contained numerous small bivalves. Presumably the filtering apparatus of *Mugil cephalus* rejects particles of such a size.

Mugil cephalus occasionally has a copepod ingested but this is probably incidental to the procurement of algae. It may be mentioned that this species, which least frequently contains zoological elements in its food, is also the least frequently caught on fishing lines. Pieces of dough sometimes tempt them in salt water, and earth-worms are useful bait in fresh water, but elsewhere animal bait is seldom, if ever, touched. Nevertheless they are not necessarily averse to animal food as large mullet have been kept successfully in the Cronulla aquarium where they were fed on chopped clam meat.

Kesteven (1942) found the gut contents of *M. cephalus* to consist of slimy mud. Mullet (*M. cephalus* and *Trachystoma petardi*) have been found in a freshwater portion of the Albert River feeding solely on green filamentous algae. Tenison-Woods (reference in Roughley 1916) found this also in New South Wales rivers. Roughley (1951) stated that

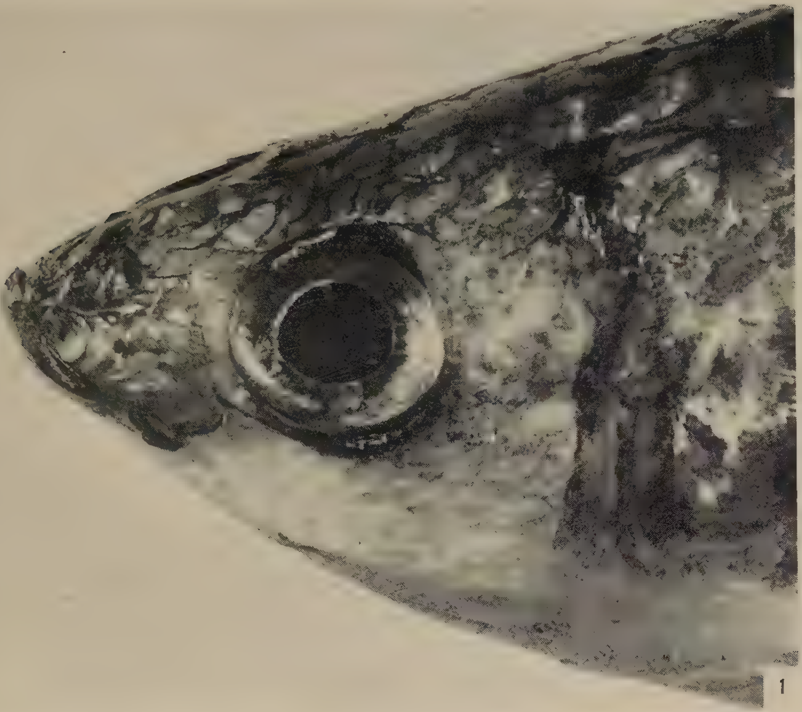
TABLE 2

FOOD OF AUSTRALIAN MULLET

Range in order of size of fish

Species	Place	Date	Size (cm)	Number	Gut Contents
Mugil cephalus					
1	Big Ck., Moreton Bay, Qld.	16.x.1952	2-3	10	Fine detrital material
2	Bonty's Ck., Moreton Bay, Qld.	26.xi.1952	4-5.5	3	Flocculent material, plant fibres; *Pleurosigma*, *Navicula*
3	Bonty's Ck., Moreton Bay, Qld.	20.xi.1952	3	2	Flocculent material, plant fibres; *Navicula*
4	Port Hacking, N.S.W.	5.x.1945	0-21	47	Much sand, grit; detritus
5	Upper Albert R., Qld.	7.vii.1951	9-5	1	Much mud, detritus, diatom chains
6	Port Hacking, N.S.W.	29.ix.1946	14-25	25	Sand, mud, filamentous algae
7	Albert R., Qld. (fresh water)	All year	5-35	100	Green filamentous algae
8	Pelican Pt., Swan R., W.A.	Jan.-Feb. 1943	14-24	70	Much sand, detritus, diatom chains
9	Tweed Heads, N.S.W.	28.i.1946	20-32	50	Green filamentous algae
10	Lake Sepping, W.A.	25.i.1948	35	1	Much mud; detrital matter
Mugil georgii					
1	Port Macquarie, N.S.W.	6.ii.1945	12	1	Copepods, algal filaments, diatoms
2	Bribie Passage, Qld.	12.iv.1949	12-13	5	Copepods, small amphipods, green and brown algae, diatoms, a little sand
3	Dunwich, Qld.	8.ii.1950	15-18	6	Copepods, filamentous algae, diatoms, a few sand grains
4	Dunwich, Qld.	11.x.1952	16	1	Copepods, brown algae, diatoms
Liza argentea					
1	Richmond R., N.S.W.	27.vi.1950	13-15	5	Very small diatoms, a few copepods, plant fibres, a few sand grains
2	Dunwich, Qld.	11.v.1951	19-21	4	Diatoms, green algal filaments, a few copepods; a little sand
3	Narooma, N.S.W.	17.x.1949	23-27	43	Slimy mud

FEEDING ORGANS OF AUSTRALIAN MULLET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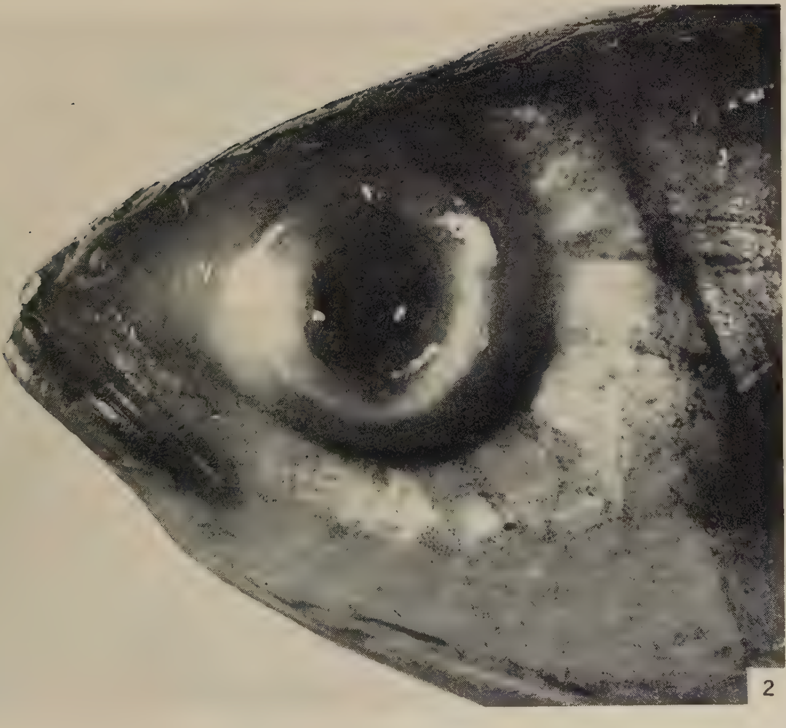
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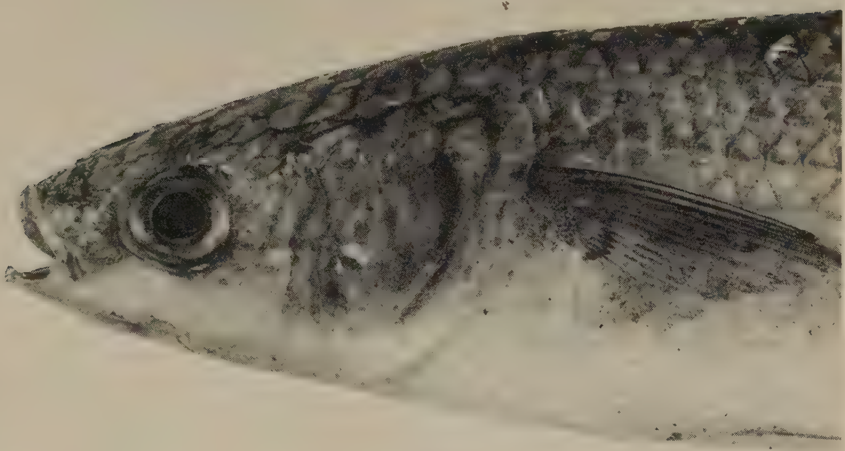
Fig. 1.—*Liza argentea* — mouth closed.
Fig. 2.—*Mugil cephalus* — mouth closed.



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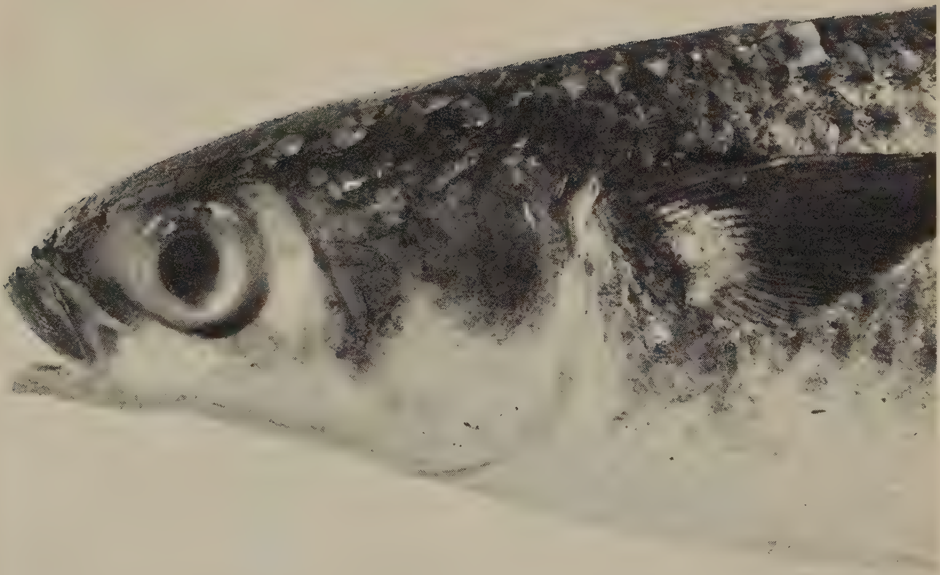

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Fig. 1.—*Liza argentea* — mouth open.
Fig. 2.—*Mugil cephalus* — mouth open.

TABLE 2 (*Continued*)

Species	Place	Date	Size (cm)	Number	Gut Contents
Liza dussumieri					
	Dunwich, Qld.	27.i.1950	19-23	13	Much sand; detrital matter, including plant fibres; a very few copepods
Myxus elongatus					
1	Narooma, N.S.W.	21.i.1949	7-16	40	Sand detritus, small bivalves
2	Port Hacking, N.S.W.	16.xii.1945	12	1	Polychaetes
3	Ballina, N.S.W.	6.vii.1950	12-17	6	Copepods
4	Port Hacking, N.S.W.	7.viii.1945	12-18	10	Grit, mud; filamentous algae
5	Port Hacking, N.S.W.	4.xii.1945	15-17	26	Much mud; filamentous algae, diatoms
6	Nambucca, N.S.W.	19.xi.1944	15-18	17	Copepods
7	Port Hacking, N.S.W.	8.ix.1945	15-18	15	Much sand, filamentous algae
Aldrichetta forsteri					
1	Denmark, W.A.	8.x.1946	12-18	10	Mud, grit, small bivalves
2	Pelican Pt., Swan R., W.A.	Jan.-Feb. 1943	12-19	70	Much sand, detritus, diatoms, small bivalves
3	Swan R., W.A.	3.xii.1946	15-20	5	Green filamentous algae
4	Augusta, W.A.	3.ii.1940	15-23	15	*Palaemonetes australis* and amphipods
5	Duke of Orleans Ck., Hopetown, W.A.	13.i.1944	16-22	11	Minute gastropods
6	Denmark, W.A.	9.v.1946	18-23	16	Sand, small bivalves
Trachystoma petardi					
	Albert R., Qld. (fresh water)	All year	4-36	60	Green filamentous algae

stomachs of *Mugil cephalus* which he has examined contained detritus and diatoms and almost always a considerable quantity of sand grains. Table 2 suggests that only mullet greater than 9 cm may ingest the long algal filaments.

Overseas observers of this species have recorded food generally similar to that recorded in Australia (Table 3).

Dill (1944) examined mullet from the land-locked Salton sea, and this unusual habitat accounts for the unusual inclusion of rotifera and cladocera in the diet.

TABLE 3

FOOD OF MUGIL CEPHALUS AS RECORDED BY EXTRA-AUSTRALIAN OBSERVERS

Author	Food Recorded
Hildebrand and Schroeder (1928)	Microscopic organisms, mainly diatoms and foraminifera, mixed with quantities of mud and vegetable detritus
Dill (1944)	Diatoms, unicellular algae (mainly desmids), blue-green algae, protozoa, rotifera, cladocera, and a large amount of sand and silt
Faouzi (1938)	Herbivores, filamentous algae, and diatoms
Lin (1940)	Organic matter, small crustaceans on muddy bottoms
Hiatt (1944)	Bottom and marginal feeder on decayed and living plant material.
Smith (1935)	Sand, mud, green algae, plant fragments, eggs and larvae of crustaceans and molluscs
Moses (1941)	Suck in mud containing decayed faecal matter
Gnanamuthu (1943)	Foraminifera
Suehiro (1942)	Much mud, small isopods, diatoms

The question of what is included in the term "detritus" is not clear. Some elements such as portions of higher vascular plants are obviously detrital, but some unidentifiable organic masses usually classed as detrital may well have been small living organisms (mostly protozoal), without skeletal elements, where distinguishing features have been obliterated on contact with the gastric juices. It is certain that the records include only recognizable elements. Equally certainly the plentiful protozoan and bacterial fauna and flora of the algae, and of the detritus, must be ingested and doubtless form a not inconsiderable proportion of the food.

Observations by various authors upon the food of other species of mullet are summarized in Table 4.

Kyle (1926) presented an unusual picture of mullet food. Either Kyle examined an aberrant species which feeds on molluscs or else an error (perhaps a confusion with red mullets) has occurred. Otherwise the foodstuffs are similar to these found in Australian species. Only some species seem to ingest any considerable quantity of metazoan (though still microscopic) animal matter (copepods, polychaetes, minute molluscs, etc.), but these also feed on algal material.

VI. CONCLUSIONS

The protrusible mouth of mullet is of the twisting-action type in which the internal hook of the maxilla forces the premaxilla outwards (Eaton 1935). The muscles involved in the protraction and retraction of the jaws are more numerous than previously stated; most herbivorous fish have serrated incisiform oral teeth and very weak pharyngeal ones (Al-Hussaini 1949); but Mugilidae have very weak teeth indeed. Those with better-developed teeth seem to include more animal food in the diet.

TABLE 4

FOOD OF EXTRA-AUSTRALIAN MULLETS (OTHER THAN M. CEPHALUS)

Author	Taxonomic Unit	Remarks on food or feeding
Beaven (1877)	*Mugil* spp.	Organic substances and very small animals
Gunther (1880)	Mugilidae	Sand and mud for the organic content
Cunningham (1896)	*M. chelo*, *M. capito*	Green and brown algae and the gravel or mud containing these and small molluscs
Jordan (1905)	*Mugil* spp.	Microscopic plants
Hornell (1911, 1921)	*Mugil* spp.	Vegetarians, debris, small crustaceans
Schroeder (1924)	*M. curema*	Stirs mud in search of food
Kyle (1926)	Mugilidae	Bivalves and univalves (mussels and rissoa) with crustacea
Hildebrand and Schroeder (1928)	*M. curema*	Minute organisms
Norman (1931)	Mugilidae	Green sea-weeds from stones and piers, but largely animal and vegetable matter in mud
Pearse (1932)	*M. curema*	Bottom mud
Ghazzawi (1935)	*M. capito*	Herbivorous, diatoms and algae
Hora (1938)	Mugilidae	Algae and minute water plants in mud
Faouzi (1938)	*M. capito*	Herbivorous, filamentous algae and diatoms
Chacko and Venkataraman (1944)	*Mugil* spp.	Plankton, diatoms, polychaetes, and brouse on vegetable matter
Mookerjee, Ganguly, and Sircar (1946)	*M. parsia*	Postlarvae feed on plankton, larger mullet on algae
Basu (1946)	*M. parsia*	Postlarvae eat plankton, large eat algae
Hildebrand (1946)	*Mugil* spp.	Mud-eating, ingested chiefly for diatom content
Pincher (1947)	Mugilidae	Green and brown algae
Al-Hussaini (1947)	*M. auratus*	Mud from bottom rich in vegetable organisms, diatoms, brown and green algae, and foraminifera
Jacob and Menon (1947)	*M. parsia* *M. vaigiensis*	Copepod feeders
Jacob and Krishnamurthi (1948)	*Mugil* spp.	Phytoplankton
Al-Hussaini (1949)	Mugilidae	Bottom feeders on diatoms, etc.
Pillay (1950)	*M. tade*	Bottom and marginal feeders on decayed and living plants

This study has not included any study of possible seasonal preferences in diet. Nor has any change in diet as size increases been noted, except that long filaments of green algae were not found in mullet less than 9 cm long.

Miss Sarojini of the Central Inland Fisheries Station, Barrackpore, India, has informed the author that in some areas she finds young mullet grazing on diatoms epiphytic on green algae; whereas the larger mullet ingest the algae as well.

Besides the recognizable elements in the food small epiphytic and epizoic forms are certainly ingested, as they abound on the natural food although their remains are unrecognizable in the gut. It seems that although some differences occur in the amount of larger microscopic animal matter ingested, in general, mullet ingest whatever organic food of suitable size is common in the area in which feeding takes place.

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FEEDING AND CONTROL OF TOHEROA (*AMPHIDESMA VENTRICOSUM* GRAY) (EULAMELLIBRANCHIATA) POPULATIONS IN NEW ZEALAND

By A. M. Rapson*

(*Manuscript received December* 21, 1953)

Summary

Surveys of toheroa stocks on the North Island beaches of New Zealand are described and the causes of natural and epidemic mortality discussed. The evidence for previous resurgent populations of tuatua (*Amphidesma subtriangulatum* Wood) alternating with toheroa is given. Analyses of water samples show that a source of sea-water rich in nutrient salts produces the great quantities of diatoms on which the shellfish populations feed. A quantitative estimation is made of the littoral phytoplankton and the dominant species are given for each beach. *Chaetoceros armatus* is found on all beaches and, in the cold months, when blooming occurs, comprises in some places 100 per cent. of the diatoms. The greatest quantity recorded is 1500 g dry weight per cu. m. of water. Each beach has a characteristic flora. The rate at which toheroa feed is determined from the diatom consumption. Methods are suggested by which more stable toheroa stocks might be developed and consequently a greater production achieved.

I. Introduction

During the years 1936 to 1949 the annual production of canned toheroa products in New Zealand amounted to about 80,000 lb. The maximum of 160,000 lb was obtained in 1941; the minimum in 1953 was only 16,500 lb. The decline occurred in spite of efforts made for many years to increase the yield. Published statistics of toheroa production are incomplete and data available for beaches worked by the two canneries are not comparable.

Ayson (1917), in a search for more commercial areas, travelled the whole length of Muriwai beach but reported that there were insufficient beds to warrant digging, while Hefford (1926) described the stock on part of the Ninety-mile beach in terms which suggested that there was an almost inexhaustible supply. The position on these two beaches was reversed by 1937 when the first of the surveys was carried out by the author (Table 2). This direct evidence suggests that the reduction of stocks on the Ninety-mile was largely man-made, while on Muriwai the almost complete absence of digging enabled stocks to be built up. Other data, however, show that major changes occur naturally.

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* Division of Fisheries, C.S.I.R.O., Cronulla, N.S.W. Field work was carried out by the author when Biologist with the New Zealand Government Marine Department.

The relatively constant commercial yield from the North Kaipara beach, which has produced about 40,000 lb of toheroa meat annually for 50 yr, shows that controlled digging is beneficial. A comparison of this beach with other toheroa-bearing areas with variable supplies should give a good guide to their productivity, and with this aim the four North Island beaches were surveyed, and observations on changes in stock and other biological conditions were made in the years 1937-45. Investigations were planned to determine the average size, age, and growth rate, the weight of meat per 100, and type and quantity of phytoplankton food available, the source of the rich nutrient salts which bring about the exceptional development of phytoplankton, and also how the latter becomes concentrated inshore. In a previous paper (Rapson 1952) the development and growth have been discussed, the remaining sections of the investigation are discussed in this paper.

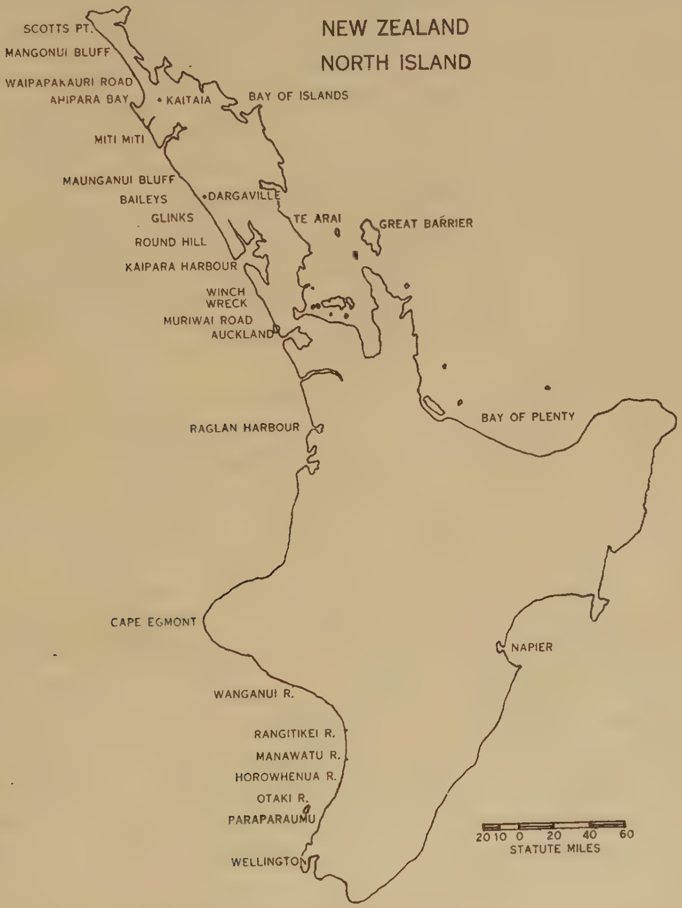
NEW ZEALAND
NORTH ISLAND
SCOTTS PT.
MANGONUI BLUFF
WAIPAPAKAURI ROAD
AHIPARA BAY
KAITAIA
BAY OF ISLANDS
MITI MITI
MAUNGANUI BLUFF
BAILEYS
DARGAVILLE
GLINKS
TE ARAI
GREAT BARRIER
ROUND HILL
KAIPARA HARBOUR
WINCH WRECK
MURIWAI ROAD
AUCKLAND
BAY OF PLENTY
RAGLAN HARBOUR
CAPE EGMONT
NAPIER
WANGANUI R.
RANGITIKEI R.
MANAWATU R.
HOROWHENUA R.
OTAKI R.
PARAPARAUMU
WELLINGTON
20 10 0 20 40 60
STATUTE MILES

Fig. 1.—North Island of New Zealand, with localities mentioned in text.

II. QUANTITY OF TOHEROA

Under favourable conditions, toheroa show marks on the beach (Plate 1, Fig. 1), and it was expected that a reasonable estimate of the number might be obtained by counting the syphon holes. On a dense bed, however, the holes are too close together to be counted accurately, as breathing movements of the shells allow liquid to escape which changes the surface markings. Plate 1, Figure 2, shows the surface of part of a bed of annelid worms (*Nephthys*) which simulate, particularly in the almost liquid appearance, densely aggregated toheroa. The *Nephthys* was obtained from a stream at the extreme margin of the dispersed area of the worm colony.

On a lightly stocked beach it was found that a bed with 20 toheroa per sq. yd. would show no syphon holes in one part, while a short distance away 80 per cent. of them showed clearly. The surface marks were clear only if the last wave on the outgoing tide was of sufficient size to wet the sand thoroughly and give the syphons sufficient time to be pushed up to the surface. Digging sample squares proved to be the only satisfactory way of finding the quantity.

Muriwai beach was surveyed in 1937, following the plan adopted by Hefford (1926) in estimating the Ninety-mile stock. The size of each bed was measured, both as to length and breadth, and the population density was found by digging several series of sample squares 2 by 2 ft from typical beds. This method cannot be used unless toheroa show well in all weather conditions. In the second method 3-5 squares were dug, at 3-yd intervals, every 0.1 mile at right angles across the toheroa zone, which usually, but not invariably, follows the half-tide contour of the beach. The quantity found and width of the productive zone are considered to be representative of the particular 0.1 mile from which they were obtained (Plate 4, Fig. 1). A car or light truck was used for most of the work, but the southern part of the Wellington Beach, which has no motor access road, was traversed in a horse-drawn cart.

The North Kaipara and Muriwai surveys of approximately 25 miles each took two men 10 days; and Ninety-mile, 55 miles, occupied two men for 12 days. The Wellington beaches with smaller numbers of shellfish took less than half the time of the other surveys. The greatest labour lay in counting and separating toheroa into two sizes, under and over 3 in. None less than 1 in. was included; this 1-in. size-group was never present in any quantity on the main beds at the time the surveys were made.

The errors in the methods used are considerable. In the running survey method employed on the Ninety-mile beach the data have been used in three different ways, which are shown separately in Table 1.

Using all the data (first column of Table 1) an estimate of the population is given, and in addition two other estimates have been made using the data from every 0.1, 0.3, 0.5 mile and 0.2, 0.4, 0.6 mile. These two latter results are independent, and the amount by which these estimates vary from the quantity obtained, using all the data, is a guide to the reliability of the method. With the exception of the quantity in the 5-10 mile section, the results of the independent estimates are within 30 per cent. of the quantity obtained using all the data as the greatest difference from the estimate in the first column. The great error was introduced by one lot of sample squares which were dug on a very dense bed and there was a rather thin irregular distribution on the remainder of the 5-mile section.

TABLE 1

NUMBER (THOUSANDS) OF TOHEROA OVER 3 IN. LONG IN EACH 5 MILES OF THE NINETY-MILE BEACH FROM WAIPAPAKAURI ROAD TO MANGONUI BLUFF

Miles N. of Waipapakauri Road	Estimate Made from Samples: Every 0.1 Mile at 0.1, 0.2, 0.3, etc.	Every 0.2 Mile at 0.1, 0.3, 0.5, etc.	Every 0.2 Mile at 0.2, 0.4, 0.6, etc.	Approximate Variation (%)
0-5	314	345	283	±10
5-10	229	327	128	±45
10-15	388	400	374	± 4
15-20	536	622	449	±16
20-25	679	647	448	± 5
25-30	1406	1606	1006	±28
	3552	3947	2688	±24

Table 2 gives the number of toheroa (calculated on the above basis) per yard length of beach, and the population under and over 3 in. In addition to these surveys, other areas were examined closely for toheroa. North of the Manawatu River for 12 miles, the beach to the Rangitikei Heads is of fine shingle and shell, and bears no toheroa. North of Bailey's Gorge on the North Kaipara, the beach can sometimes be travelled for 13 miles to Mangonui Bluff, but on three occasions this area was found to have only two or three small beds per mile, and it is frequently not trafficable after the first 3 miles. On the Ninety-mile beach the extreme northern 15 miles from Mangonui Bluff to Scott's Point is a wide flat sandy beach, which in 1939 carried small stocks along its whole length; but these had practically disappeared in 1940.

Although the populations of toheroa are continually changing the surveys form a sound basis for comparing the productivity of one year with another. They were carried out firstly to determine the actual numbers of toheroa on each beach so that, in conjunction with other data, an estimation could be made of the quantity of meats which might be obtained, leaving a safe working margin. As a working guide which under favourable conditions can be obtained in several hours by one man with a car, it has been found that from eight to ten beds, each 50 yd long and occurring every mile, represent excellent conditions; five to seven such beds represent good, and one or two beds poor conditions. A large number of beds with a moderate density of 100-150 per sq. yd. in the thickest parts, are more satisfactory that a few densely populated areas. Muriwai beach in 1937 carried a population of toheroa which for many miles had never been dug: 620 medium and large, 2½-4½ in. long, per sq. yd. were obtained here on one bed which extended almost unbroken for 1200 yd. There were, however, many barren parts and the first 10 miles carried rather reduced stocks. On the Ninety-mile beach in 1939 the large numbers obtained on some parts were under 2 in. long. The greatest density of all beaches was on the North Kaipara near Tekopuru Rock, where 810 large toheroa per sq. yd. were obtained in 1940 and, from small sample squares 3 by 4 in., more than 100 toheroa less than 1 in. long were obtained from this beach on four occasions (see also Weymouth, McMillin, and Holmes 1925).

TABLE 2

RESULTS OF SURVEYS 1937-40. NUMBER OF TOHEROA PER YARD LENGTH OF BEACH IN APPROXIMATELY 5-MILE SECTIONS, AND POPULATION UNDER AND OVER 3 IN. LONG FOR FOUR BEACHES

Beach	Miles N. along Beach*						Population (millions)		
	0-5	5-10	10-15	15-20	20-25	25-30	Over 3 in.	Under 3 in.	Total
Wellington Waikanae to Manawatu R. March 1940	—	28	62	131	119	—	2.4	0.2	2.6
Muriwai Nov. 1937	—	78	107	451	673	80	6.7	8.5	15.2
North Kaipara from Round Hill Nov. 1938	352	228	212	80	106	—	4.1	5.0	9.1
Ninety-mile Nov. 1939	87	52	103	331	559	521	1.4	10.6	12.0

* For the Ninety-mile and Muriwai beaches, which have few natural divisions or landmarks, the distances are given in exact 5-mile sections. For Wellington and North Kaipara, however, natural boundaries have been used to divide the beaches as follows: Waikanae 0-8 insufficient for survey, 5.5, 4.5, 3.5, 4.7. Total 26.2: North Kaipara 6.0, 5.5, 4.6, 5.9, 3.9. Total 25.9.

The reduction in stocks on densely populated beaches may be rapid: Coe 1953 cited variations in populations of *Donax* at La Jolla, California. In 1952 in a period of a few days the stock was reduced from 10,000 to 20 individuals per sq. m.

III. PREDATORS AND MORTALITIES

The small shore gull (*Larus novaehollandiae* Steph.) is common on all beaches. By paddling in the streams it obtains young toheroa which come to the surface, although its usual food when feeding in this way consists of crustaceans. Black-backed gulls (*Larus dominicanus* Lich.) which are usually less common, eat only the toheroa left stranded on the surface of the sand, or those incompletely covered. The shell is broken when the bird drops it from a height 80-100 ft. These birds have difficulty in picking up toheroa over 4½ in. long, weighing about 7 oz, because of the smoothness of the shell. In 1937 a colony of about 200 was nesting in the sandhills a short distance above high water on Muriwai beach, approximately 10 miles from the road. Only a few birds remained after January 1938, when dead toheroa were not plentiful.

TABLE 3

MAJOR MORTALITIES OF TOHEROA

Date	Locality	Remarks
28.iv.30 to 5.v.30	Ninety-mile, 10-20 miles N. Ninety-mile, 10-20 miles N.	Easterly gales made deep sand drifts on the beds
30.x.30		Snapper reported with toheroa tongues in stomachs
7.ii.32		For several hot days tides did not cover the toheroa beds
2.iii.32	Ninety-mile	
Jan. 1938	All beaches	
Nov. 1938	North Kaipara Muriwai Waiterere	Not a true mortality: shellfish lethargic. Period of calm cool weather, lack of oxygenation of water a possible cause
May 1945	Ninety-mile	Toheroa and tuatua with syphons and tongues bitten off or with longitudinal teeth marks in the tongues

Snapper (*Chrysophrys auratus* (Bloch & Schneider)) can at times be seen in the surf digging for toheroa; the fish swim vertically downwards, and during big waves they are able to obtain the whole shellfish. Teeth of snapper which feed on toheroa are usually worn down at an early age. Small fish attack the shellfish only when they are being washed about in the sea, and toheroa with syphons and tongues bitten are occasionally found. On several occasions these mutilations have been reported on a large scale, and this has been considered as a cause of epidemic mortality; such happenings may take place when a bed of toheroa has been washed out by the surf. Boring gastropods which attack lamellibranchs (see Smith 1932) have not been observed on toheroa.

Since 1926, through surveys and visits by many interested people, much information has been gathered on mortalities of toheroa. The occurrences and relevant remarks concerning the principal periods of mortality are given in Table 3, and Plate 2, Figure 1, shows the extent of the deaths on Waiterere beach in 1938. The variety of causes indicates that possibly none of these mortalities has been due to epidemic disease. As similar exceptional deaths are a common occurrence in other countries, the following list of symptoms discovered from an examination of dead and dying toheroa on the Wellington beach in January 1938 is given:

(1) Sensitivity of inhalent syphon and mantle remained until decomposition was well advanced.

(2) The large adductor muscle was weak and its tissues were partly broken down, apparently by bacterial action. This lack of power had the effect of letting the gills become clogged with sand, and allowed the shells to gape, which left the animal open to attack by sandhoppers (*Talorchestia*). Other muscles and fleshy parts were not affected so much.

(3) Cilia at the anterior part of the gut continued to move freely, even after the animal was classed as putrefying.

(4) Gonads contained normal eggs, or sperms motile in sea-water.

(5) The liver was usually partly liquid and in most specimens examined one or more protozoans (*Stylonichia*) were found (see also Coe 1953 and Wenyon 1926).

(6) Stomachs often contained grass seeds which had been blown on to the water, and the lack of muscular control of the inhalent syphon filter permitted their entry.

Toheroa are among the more active of the clam group, but on several occasions a marked decrease in their normal activity was observed in calm weather. Plate 2, Figure 2, shows toheroa on Muriwai which were unable to cover themselves completely with sand during a calm, and Plate 3, Figure 1, shows a typical "lethargic" toheroa taken in November 1938. The syphons remained extended and the tongue made only feeble efforts to dig into the sand. Pricking tongue, mantles, and syphon did not cause these organs to be withdrawn into the shell; a similar lack of response was found during the January 1938 mortality. Mitchell (1912) estimated that oysters and mud clams require only small amounts of oxygen, but the coincidence of toheroa mortality with lessened surf (excluding the effects of depredations of fishes) suggests that there is a relationship between the physical condition of the sea or beach and toheroa mortality. Oxygen requirements of active clams, which must anchor themselves in shifting sand, will be greater than for sedentary mud dwellers or sessile oysters, and the change from water thoroughly aerated and possibly supersaturated in oxygen in the most violent part of the littoral surf zone, to water of a lower saturation may be expected to have some effect on these shellfish.

Poisonous dinoflagellates which are also known as "red tide" may kill shellfish; they were not found in any sample of plankton on the west coast beaches, but *Gymnodinium* occurred in Wellington Harbour in February 1936, and at French Pass in August 1937, so that these organisms must be included as a possible cause of mortality.

Orton (1934) said of *Cardium edule* that parasitism and the effect of sudden rises in temperature on spawning individuals may be causes of mortality; while Gunter and Hilderbrand (1951) said that, in the cold waves which sometimes destroy marine life on the Texas coast, the rapidity at which the temperature falls, rather than the degree or duration of coldness, determines the effect. Kellog (1903) referred mortality of small clams on a densely populated bed to starvation, while mature clams some distance away escaped. Chen and Kao (1936) reported that razor clams die of starvation when the density of water reaches 1.018-1.020, because the diatoms *Pleurosigma affine*, on which they feed, die in water of this density.

Investigations in New Zealand have shown that both large and small toheroa are able to survive when supplies of diatoms are almost negligible; so that a scarcity of diatoms is not a direct factor. The food cycle of toheroa is remarkably constant, and all mortalities have occurred, as far as is known, at a time when a considerable variety of organisms was present in the plankton, but not during phytoplankton blooms in which only a few species are found.

With the possible exception of the mortality of January 1938, which may have been caused by the sudden rise in beach temperature when the tide did not cover the toheroa, mortality was almost certainly caused by a combination of circumstances which may include lack of surf, increased temperature, change in food supply, and poor condition due to spawning or starvation. No one factor alone was known to have serious effects. In November 1938 toheroa were in good condition and in spite of the change in food and lack of surf no mortality occurred.

The records of old settlers living near the Ninety-mile beach show that about 1900 there was a period of great scarcity of toheroa, but after this time they were in reasonable abundance, except for some local shortages, until 1938. A major change which occurred during 1939-45, however, is still not satisfactorily explained; the stocks were reduced by mortality and by commercial exploitation. It appeared as if tuatua (*Amphidesma subtriangulatum* Wood) in greater abundance and living in the sand over the toheroa, were able to eliminate the latter species as if by smothering. Tuatua secrete a liquid which makes the sand slimy; this may cause toheroa to move away or even to die. Toheroa are rarely found mixed with tuatua. Extensive shell deposits which occur on the Ninety-mile beach show that vast numbers of shellfish have populated the beach previously. In the sand dunes toheroa and tuatua are found together, although 80 per cent. of some deposits are composed of tuatua and other deposits consist almost entirely of toheroa. Some of these shell heaps appear to be natural deposits, while others show evidence of Maori habitation.

An exposed face of shell over 4 ft high (Plate 3, Fig. 2) at Mangonui Bluff is part of a deposit composed entirely of tuatua, 1½-2½ in. long. It is the remains of a population similar to that which inhabited the Ninety-mile beach in 1945. The geological formation is recent, but there is no information available to show whether the deposits were formed within the last 100 years or a great many years ago.

The cycles of abundance and scarcity of the two species have similarities to the resurgent populations of *Donax* described by Coe (1953) on the North American Pacific Coast, but in New Zealand there are alternating resurgent populations of toheroa and pipi.

The large populations of toheroa, which may be more than 500,000 per mile (or up to 5,000,000 tuatua per mile), require for food great quantities of phytoplankton; the supply which develops during the winter months suggests a source of nutrient salts much richer than is to be found in the off-shore waters of the Tasman Sea.

IV. THE INSHORE WATER

Off the west coast of New Zealand there is a north-easterly current (New Zealand Pilot 1919; South Pacific Ocean Currents 1910-1937; Sverdrup, Johnson, and Fleming 1942). It is, however, not well defined and calculations on its strength made from data in South Pacific Ocean Currents (1938), show that at a distance of 150-200 miles off shore the speed in miles per day is:

Nov.-Jan. 1.7; Feb.-Apr. 1.6; Mar.-July 4.2; Aug.-Oct. 2.3.

Closer inshore there is less information, the prevailing winds, however, which are from north-west to south-east, blow hardest in winter, easterly winds blow in summer (New Zealand Pilot 1919). These have been observed as early as October and sometimes produce strong currents. Several miles off Hokianga (South Pacific Ocean Currents 1938) there is a westerly current of 10.5 miles per day during February to April. The effect of these winds and currents on toheroa is discussed after consideration of other hydrological data.

TABLE 4

CHEMICAL COMPOSITION OF THE OCEAN CURRENT OFF AUSTRALIA AND OFF THE WEST COAST OF NEW ZEALAND. PHOSPHATE AS P IN MG/CU. M.

	East Australian Current* Jan. 1941					New Zealand West Coast Current† June-July 1932				
Station No.	60	45	31	19	15	923	924	925	926	928
South Latitude	42°	38°	35°	30°	28°	47°	44°	41°	38°	34°
Temperature (°C)	15.4	18.6	19.7	24.5	24.6	8.9	11.4	12.1	14.2	14.9
Phosphate, surface	35.2	35.4	35.5	35.5	35.5	34.4	34.8	34.9	35.4	35.4
Salinity (°/₀₀)	4	4	8	3	2	38	23	20	17	20
Phosphate, 150 m	10	17	13	10	8	40	34	29	28	31

* Oceanographical station list 1951, C.S.I.R.O. Division of Fisheries, Vol. 2, pp. 70-98.

† Discovery Report Station List 1942. Vol. 21, pt. 1, pp. 112-14.

Table 4 summarizes information on water analyses off the New Zealand west coast from the surface to 150 m (Discovery Station List 1942) and for comparison a similar series is included from off the east Australian coast (Oceanographical Station List 1951). In order to determine if the higher concentration of phosphates in the New Zealand coastal waters had come from the land a series of analyses was made of water from lakes, streams and onshore sea-water obtained from various beaches. Results are given in Table 5. The relatively small quantity of phosphates in lakes and streams shows that the rich supply does not reach the sea from this source; although the Manawatu River, near Waiterere, drains good farm lands and small quantities of phosphate may also reach the sea from seepage water in this region the quantity is not great (compare 41°-44°S., Table 4). The appreciable quantity found in seepage water, particularly on the North Kaipara beach at Glinks Gap, probably originates from buried phytoplankton, which decomposes, the salts being returned to solution. It is not uncommon to find on this beach extensive areas in which the sand dug from toheroa beaches is blackened by decaying phytoplankton which also colours the shells black. This is probably similar to the decaying organic matter described by ZoBell and Rittenberg (1948) who discussed the presence of sulphate-reducing bacteria in the sea. Toheroa do not appear to be harmed by rotting plankton, although the buried deposits are often foul-smelling. The difference in salinity of the seepage water on Muriwai and North Kaipara beaches indicates that water of a wide range of salinity may remove phosphates from the rotting diatoms, and a rapid interchange between the beach and ocean would occur by the action of the waves and filtering action of the sand. If allowance be made for increase in salinity can be seen to vary considerably, but such a condition is to be expected from fresh water to sea-water the phosphate equivalent for sea-water from the great variability of the diatom deposits on the beach.

The chemical composition of the three types of water during the summer period of phytoplankton was not determined, but the decline in diatom population in spring is brought about by the easterly winds. The inshore water and diatoms are blown seawards* and a great variety of zooplankton supersedes. The water analyses in Table 5 were from collections made in July at a time when prevailing westerly winds might be expected to be blowing surface water from the Tasman Sea to the coast. Easterly winds, which would produce a vertical circulation from the bottom with a supply of nutrient salts in summer, do not allow the phytoplankton to develop inshore as the upwelled water is blown out to sea.

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* Jespersen (1935) related decreasing volumes of plankton across the Tasman Sea to increase in temperature but made no reference to the richer water off the New Zealand coast.

TABLE 5

CHEMICAL COMPOSITION OF WATERS AFFECTING TOHEROA BEACHES. PHOSPHATE AS P, NITRATE AS NO_3, MG/CU.M.

Location	Stream and Lake				Seepage				Inshore Ocean Water			
	Temperature	Salinity ($^0/_{00}$)	Phosphate	Nitrate	Temperature	Salinity ($^0/_{00}$)	Phosphate	Nitrate	Temperature	Phosphate	Nitrate	Salinity ($^0/_{00}$)
Tepaki, Oct. 1939	22.2	0.7	11	70	17.0	19.5	23	8	17.1	9	5	35.1
Mangonui Bluff, Oct. 1939	19.2	0.1	9	40	21.8	3.0	23	100	17.8	18	6	35.2
Waipapakauri, Oct. 1939	21.8	0.1	0	8	20.0	35.0	13	8	17.8	9	7	34.9
Glinks, May 1939	—	—	—	—	16.9	4.7	72	80	—	—	—	—
Muriwai Heads, Oct. 1939	—	—	—	—	—	—	—	—	17.0	11	8	33.4
Muriwai Rocks, Oct. 1939	16.6	0.2	0	15	16.4	21.1	41	5	14.2	36	8	34.1
Waiterere, July 1938	9.2	0.2	23	200	12.9	28.2	41	20	11.2	9	24	30.5

Origin of the water which upwells on the coast is unknown (see Deacon 1937). It is suggested, however, that conditions off the North Auckland west coast resemble on a small scale the Humboldt Current of the west coast of South America and the Benguela Current on the west coast of South Africa, both of which are biologically much richer than the New Zealand current. There is a depth of 400 fm half a mile off the North Kaipara beach, and the extremely steep bottom contour helps to concentrate upwelled water into a confined space, so creating favourable conditions for the development of phytoplankton.

There are two important effects of the west coast current and prevailing west wind on the toheroa:

(1) The poor stocks to be found on the southern end of each beach, in some cases, can be ascribed to human activity, but an examination of the northern ends shows that supplies, although sometimes not plentiful, are usually more abundant than on the southern end. This applies to the four principal beaches and is most pronounced on the southern end of the North Kaipara, which bears no toheroa for many miles north of the Kaipara Heads, whereas on the Muriwai beach they often occur on the South Kaipara Head. The southern ends of toheroa beds on many miles of beach are sometimes rounded whereas the northern ends are elongated, making the beds pear-shaped and indicating a stronger set to the north than usual. The contrary effect has never been observed. The normal tidal flow is north and south, which produces a distribution of larvae over a wide area, but the northern drift can be expected to leave the southern parts of all beaches with small stocks.

(2) The most striking effect of the west wind is the concentration of phytoplankton inshore during the winter. The continuous strong wind and heavy surf acting on wide sandy beaches make the sand act as a filter, and a considerable part of every wave, especially on the incoming tide, seeps through the sand so that the plankton, which tends to float, is concentrated. After six tides on a toheroa beach it is estimated that all the inshore water in the tidal zone has been filtered.

Plate 5, Figure 1, shows an incoming wave with phytoplankton being concentrated, and Plate 4, Figure 2, shows an extensive beach deposit, in some places 1 in. thick. The dominant species in the phytoplankton is *Chaetoceros armatus* Westendorp.

V. QUANTITY OF PHYTOPLANKTON

As collecting with a boat and tow net was not practicable for the quantitative estimation, samples were taken by wading into the sea to a depth of about 2 ft. When there was only a small quantity present an N50 Discovery net was used and one or more nets full of water were filtered by slowly lifting the net out of the water. When there were greater quantities several gallons of water were poured through a strainer about 4 in. in diameter and depth, made of bolting silk of 200 meshes per in.

During phytoplankton blooms a half-gallon jar of water was collected, preserved with formalin, and allowed to settle, when the liquid was poured off. As personal error could seriously affect results obtained by this method, small dense blooms were avoided, but it was not always easy to judge the dense areas, because, at times, floating patches had little underneath, whereas green water at a depth of 2 ft sometimes contained about one-fifth (settled volume) of phytoplankton. (See also Winsor and Clarke 1940.) An examination was made for the principal species and the formol-preserved material or a fraction of it was transferred to a tube and given three washings with a quantity of fresh water equal to 10 times the settled volume of phytoplankton. The sand and shell which quickly settled were separated by decanting the phytoplankton, which was then allowed to settle for 24 hr between washings. After the third washing water was poured off, the tube and contained phytoplankton were dried at a temperature of 80°C to constant weight.*

TABLE 6

AVERAGE QUANTITY OF PHYTOPLANKTON TAKEN 1938-44 WITH 200 MESH PER IN. NET, GIVEN AS DRY WEIGHT (G PER CU. M.) OF SEA-WATER

Number of samples in brackets

Period	Ninety-mile	North Kaipara	Muriwai	Wellington	Western Cook Strait, Upper 2 m
Jan.-Mar.	1.6(2)	2.3(6)	0.5(3)	0.2(5)	0.1(4)
Apr.-Sept.	1.8(21)	102.4(18)	12.2(10)	8.9(11)	0.2(3)
Oct.-Dec.	0.4(4)	3.1(13)	1.7(4)	9.8(14)	0.1(3)

There was considerable variation in the ratio of settled volume to dried weight, and the former is not given. It is considered, however, that the dried weights contain no error due to salt; fine particles of sand may have increased the minimum results, but were not apparent in the average or higher quantities obtained. The results are summarized for the four beaches; some samples from Cook Strait are included for comparison to show the effective manner in which the phytoplankton is concentrated by the continued action of the surf on the sandy beach. Riley, Stommel, and Bumpus (1929) gave the range in number of diatom cells in the western North Atlantic from 60 to 7400 cells per ml. Inshore water on the North Auckland west coast showed a variation from 0 to 10^5 cells per ml. The large quantity was not obtained from the concentrated patches. It consisted of *Chaetoceros armatum* in single cells and chains up to 35 (average 6) cells long.

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* Although the method employed to collect phytoplankton appears inaccurate by other standards, some of the recent plankton samplers described have disadvantages which make them unsuitable for collecting on the west coast. Clarke and Bumpus (1940) described a net with mechanism to measure the volume of water filtered but King (1950) has shown difficulties connected with this method as fine nets become clogged and in heavy waves the plankton is washed out.

The greatest quantity obtained was from the North Kaipara beach in August 1942, when the inshore sea-water contained 1505 g dry weight of phytoplankton per cu. m., a similar bloom, however, occurs every year. Other samples from the same beach at this time were 5.5 g on the extreme southern boundary of the toheroa beds, and 243 g north of Glinks. When phytoplankton is left on the beach (Plate 4, Fig. 2; Plate 5, Fig. 1) over many miles extremely high concentrations occur (see also Clarke 1937), but with the exception given above such dense phytoplankton is not included in Tables 6 and 7.

Although the dense flowering may extend for many miles, the limits are usually clearly defined, and the northern and southern ends can be seen like the off-shore boundary, which is usually less than 400 yd from the beach. In August 1942, the area extended approximately 28 miles. The quantity of phytoplankton in this "bloom", estimated for a width of sea of 100 yd, and for an average depth of 4 ft, at 300 g per cu. m., was more than 1500 metric tons (dried weight). A large part of the phytoplankton was at times left on the beach. By comparison, other beaches produce small quantities (Table 6, April to September), and the surface waters of Cook Strait are almost barren. Two nil quantities obtained on Muriwai beach were omitted. They were collected near low water during non-flowering periods in the vicinity of dense beds, and although there is little doubt that the filtering effect of a large population could extract all the diatoms from a considerable volume of water, it is probable that in these two cases seepage water filtered by the sand was collected. It was not possible to collect all samples at the same stage of the tide. Nikolskii (1950) compared the organic matter in sea-water at 5 g/cu. m. with that in different types of soil containing 14-25 per cent. On the basis of wet weight the dense phytoplankton makes the sea-water comparable to soil with the lowest organic content.

Phytoplankton deposited on the Wellington beaches is seen as an extremely thin film extending over a wide area, and the long period during which relatively large quantities occur (April to December) suggests a more regular occurrence than on the northern beaches.

Previous accounts of toheroa populations on the Ninety-mile show that at times this beach must be well suited for their needs. The food supplies during the period under observation, however, were the smallest from any beach. The largest quantity recorded was 5.6 g/cu. m. (August 1941), and the smallest 0.04 g/cu. m. (August 1940). By this time tuatua had already made their appearance on the southern end of the beach. It is believed that their feeding reduced the phytoplankton to the low quantity found. North Kaipara has by far the greatest quantity of phytoplankton and the Ninety-mile the smallest; the small regular quantities found on the Wellington beaches indicate that this coast contains a slightly better supply than the Muriwai, but if the food requirements of the larger Muriwai population of toheroa are considered Muriwai is by

TABLE 7

SUMMARY OF RESULTS OF SURVEYS, A SUGGESTED OPTIMUM POPULATION OF TOHEROA, AND AN ESTIMATE OF THE ANNUAL PRODUCTION OF MEAT CALCULATED FROM THE GROWTH RATE AND THE QUANTITY OF PHYTOPLANKTON

Beach	Length (miles)	Calculated Optimum Population Over 3 in. (millions)	Phytoplankton (g per cu. m. dry wt.)			Weight of Meats per 100 Observed (over 3 in.) (oz)	Average Growth per Year (in.)	Estimated Production of Meats (1000 lb)
			Maximum and Date	Minimum and Date	Average			
Ninety-mile	30	15.0	5.6 Aug. 1941	0.05 Nov. 1939	1.4(28)	75	0.7	60
North Kaipara	20	4.0*	1505† Aug. 1942	0.9 Nov. 1939	59.9(39)	95	0.9	40
Muriwai	25	5.0	72.1 Aug. 1940	0.4‡ Mar. 1940	6.6(15)	80	0.7	30
Wellington	25	3.0	54.2 Oct. 1941	0.07 Apr. 1940	6.9(21)	150	0.6	20

* It is unlikely that larger stocks will develop because of the nature of the beach.

† One sample of 1804 g omitted.

‡ Two nil samples omitted.

far the more productive. In Table 7 production is given for the four beaches, North Kaipara, Ninety-mile, Muriwai, and Wellington. The stock of toheroa on a beach is not influenced greatly by minimum supplies of diatoms, as shellfish appear able to exist for some weeks (if not months) when there are extremely small quantities of phytoplankton.

The amount of food in a toheroa stomach could not be directly determined with accuracy from an examination of the stomach because the diatoms are present in a quantity of liquid digestive fluid, usually about 3 ml for a 4-in. toheroa. An experiment was carried out on several occasions to determine the rate at which diatoms were consumed, as toheroa circulate water and feed when great quantities of diatoms are present. Only once was the test successful. A 4-in. toheroa obtained from the beach shortly before the tide covered the beds was placed in a jar with sand plus 500 ml of sea-water rich in phytoplankton. The average number of colonies of *Chaetoceros armatus* per microscope field was obtained from 3 or 4 drops taken at 5-min intervals for 50 min. The results obtained (the first figure represents the number of colonies before toheroa was placed in the jar) were: 290, 115, 104, 86, 62, 45, 44, 41, 41, 40, 46. During the first 5 min the reduction in numbers shows that the 500 ml of water was circulated and diatoms extracted. A similar reduction also occurred in the succeeding 15-20 min, although there did not appear to be any reduction in the rate at which the water was circulated as seen by the movement of diatoms near the syphons. The extraction of diatoms had practically ceased after 30 min but water continued to be circulated freely during the whole period of the experiment. The increase in number of colonies after 45 min was caused by the breaking of the larger diatom chains.

In summer, when phytoplankton is scarce, the source of toheroa food gives rise to much speculation. As toheroa are not known to succumb to starvation there must be other types of food. Observations on the beach show at least two possible sources:

(1) The decomposition of phytoplankton may produce a large population of bacteria suitable for food;

(2) The large numbers of ctenophores, scyphozoa, and salps which sometimes occur in summer and are broken up in the surf, may be used as food. On two occasions a thin gelatinous film covering many miles of beach was found on dry sand; this substance was evidently not in solution in the sea-water before being deposited, and if not used directly as food by toheroa it may act as a nutrient medium to produce bacteria (see also Coe 1948).

The evidence from the quantitative data on diatom food available for toheroa shows an excess in winter on the North Kaipara which is not utilized, and for the relatively small population more than twice the quantity is present in summer than on other beaches. The minimum quantity obtained on the Ninety-mile beach, 0.05 g/cu. m., is due to a large tuatua population. With the varied information available an attempt is made in Table 7 to show the quantity of meats which may be expected with the stocks maintained at a reasonable level of productivity. The calculation was made as a simple proportion on the basis of the North Kaipara beach, allowing for length of beach, population, weight of meats, and average growth (see Rapson 1952). The factors used for food supply were Muriwai 0.3, Wellington 0.4, and Ninety-mile 0.5. It is considered that the tuatua population was sufficient to reduce the phytoplankton on the latter beach.

The amount of phytoplankton available for harvesting, if a use could be found, is considerable. Juday (1943) gave the chemical composition of some algae and discussed food values. Hardy (1941) said that phytoplankton has a food value comparable to rye flour but that it would be uneconomic with fleets of nets to collect plankton. Shropshire (1944) indicated the economic possibilities and gave a design of a machine which produced 1 g of wet plankton cake from 16 gal of water. The yield which might be expected from the North Kaipara beach during blooming is approximately 1 g dry weight plankton from 2 gal of water.

Air-dried phytoplankton was characterized by a faintly unpleasant smell as if decomposition had commenced, and in such circumstances did not appear suitable as a foodstuff, but animals might eat it. A much better product was obtained with washed phytoplankton dried at 80°C (see Clarke and Bishop 1948). A chemical test for iodine showed only negligible quantities to be present.

VI. The Phytoplankton Cycle

The composition of the phytoplankton on the North Kaipara beach is given (Table 8) for several periods from 1938 to 1939. Observations were made for several days every 3 months. The percentages were obtained from an examination of four or five representative microscope fields for each sample. *Chaetoceros armatus* as colonies is the dominant species in all samples, except the first recorded on November 8, 1938, which contained exceptional numbers of *Thalassiothrix nitzschioides* Grun. and minute crustacean larvae. *Asterionella japonica* Bail. (and usually *Biddulphia sinensis* Grev.) were present except during the months of flowering. Coscinodiscinae were dominant as a family in February 1939 but were not in abundance in other years. In the group "others" are included *Rhizosolenia imbricata* Brightwell, which comprised 4 per cent. on one occasion, *Nitzschia seriata* Cleve, and peridinians, none of which exceeded 3 per cent. Although Coscinodiscinae are eaten by toheroa, most of them are not digested and some appear to be viable after passing through the alimentary canal. The dominant *Chaetoceros* in May and August is typical of the phytoplankton on this beach during the winter months each year. It was expected that samples taken to the south of Glinks Gap would be a guide to the phytoplankton at Glinks 1 or 2 days later, but results

TABLE 8

CYCLE OF CHANGES IN PERCENTAGE COMPOSITION OF THE PHYTOPLANKTON ON THE NORTH KAIPARA BEACH ABOUT GLINKS GAP, 1938-39. CHAETOCEROS AS COLONIES, OTHERS AS SINGLE CELLS

Date	*Chaetoceros armatus*	*Asterionella japonica*	*Biddulphia mobilensis* (etc.)	*Thalassiothrix nitzschioides*	Coscinodiscinae	Others	Remarks
8.xi.38	3	4	—	35	8	50	10 Miles south of Glinks
9.xi.38	79	—	1	3	15	3	
10.xi.38	82	1	1	2	10	1	
20.xi.38	35	—	3	9	47	3	12 Miles south of Glinks
25.ii.39	61	—	3	—	25	1	
26.ii.39	85	10	1	1	2	1	
1.iii.39	87	2	1	—	10	—	
2.iii.39	65	32	—	—	2	1	
12.v.39 to 15.v.39	100						4 Samples
16.viii.39	100						
16.viii.39	100						5 Miles south of Glinks
18.viii.39	88	1	5	—	6		
13.xi.39	92	3	2	—	5		
14.xi.39	64	31	1	—	4		20 Miles south of Glinks

did not bear out this theory and changes which occur in the composition from day to day evidently originate off shore.

Table 9 gives the percentage of different organisms for the North Auckland beaches for May 1944 and for Wellington in October 1940. The data are fairly typical and comparable except that at Muriwai Rocks a much greater variety is obtained and at South Kaipara Heads less variety is usually found. Peridinians and crustaceans have been omitted. The sample from the North Kaipara beach corresponding to the South Kaipara Head is from approximately 20 miles north of the Harbour entrance (the limit of the range of Kaipara Harbour water). The Muriwai flora was found to be more varied than on other beaches and some species found there evidently were either unable to pass the Kaipara Harbour entrance or could not survive in competition with the dense *Chaetoceros armatus.* These included *Stephanophyxis turris* (Grev.), *Ditylium brightwelli* (West), and *Lithodesmium undulatum* Ehr.

In Table 10 all the data available for the months of flowering are combined for each beach. *Asterionella* appears to be a more important form than *Chaetoceros* on the Wellington beaches but *Chaetoceros* in chains of five or six is still dominant. *Melosira,* which represents 10 per cent. of the Muriwai flora, was recorded only on one occasion during 1938-39 on the North Kaipara. It was, however, usually found near Muriwai Rocks. Tables 8-10 indicate that, while each beach is to some extent influenced by currents which may change the inshore diatom fauna in the course of a single tide, there is a type of flora for each beach which consists predominantly of *Chaetoceros armatus* and *Asterionella japonica,* the respective proportions of which can be regarded to some extent as typical for each beach. Muriwai and the Wellington beaches show the greatest variety. A great many other diatoms were found than are mentioned in Tables 8-10. Reference has been made only to species which comprised more than 1 per cent. of the phytoplankton of the individual samples in Tables 8 and 9 and in the average for Table 10.

Phytoplankton usually first appears off shore, and it may remain there for some days and occasionally weeks before it comes close enough inshore for the toheroa to feed on it. The development of the first bloom may, however, occur suddenly, and toheroa, even in the large numbers which exist, are quite unable to consume all of it so that much is left on the beach. The phytoplankton, which can survive considerable desiccation, sometimes has a frothy consistency (Plate 4, Fig. 2; Plate 5, Fig. 1) and may then be stranded to a depth of over an inch; the setae of the cells appear able to draw up moisture from the beach and the whole mass is kept moist. At other times the thick plankton is left as a more solid mass, and may dry appreciably, but it has never been found in a desiccated condition. The black slime found on toheroa is caused by rotting phytoplankton and may remain for many months, it wears off first at the widest

TABLE 9

PERCENTAGE OF DIFFERENT ORGANISMS FROM VARIOUS BEACHES IN TYPICAL SAMPLES OF PLANKTON. CHAETOCEROS AS COLONIES, OTHERS AS SINGLE CELLS

Species	Ninety-mile			North Kaipara			Muriwai			Wellington		
	Scotts Point 18.v.44	Hukatere 18.v.44	Waipapakauri 18.v.44	Baileys 11.v.44	Glinks 10.v.44	Round Hill 9.v.44	South Kaipara Head 21.v.44	Winch 20.v.44	Rocks 22.v.44	Manawatu 29.x.41	Waiterere 16.x.40	Hokio 14.x.40
Chaetoceros armatus	91	78	96	98	100	84	13	44	80	92	90	88
Chaetoceros spp.	2	10	2	—	—	2						5
Asterionella japonica	2	—	—	—	—	6	41	—	—	8	—	4
Thalassiosira subtilis etc.	—	—	—	—	—	5	4	14	20	—	—	—
Coscinodiscinae	2	—	—	1	—	3	8	26	—	—	2	—
Rhizosolenia robusta	—	—	—	1	—	—	2	—	—	—	—	—
R. imbricata	3	4	2	—	—	—	—	—	—	—	—	—
Thalassiothrix nitzschioides	—	8	—	—	—	—	8	—	—	—	—	—
Fragilaria	—	—	—	—	—	—	—	3	—	—	—	—
Lithodesmium undulatus	—	—	—	—	—	—	3	3	—	—	—	—
Biddulphia												
B. mobilensis	—	—	—	—	—	—	—	3	—	—	—	—
B. sinensis	—	—	—	—	—	—	19	4	—	—	—	—
Ditylium brightwelli	—	—	—	—	—	—	2	2	—	—	—	—
Stephanophyxis turris	—	—	—	—	—	—	—	2	—	—	—	—

part; the white membrane covering the new shell is not stained so there is left a curved black band over each shell.

The plankton cycle on the west coast is apparently influenced in three different ways:

(1) The west wind blowing for most of the year builds up inshore the characteristic phytoplankton flora in which zooplankton forms generally do not thrive.

(2) During the easterly winds in October this cycle is changed and zooplankton dominates inshore; its origin at times is almost certainly from as far south as Cook Strait.

(3) Not infrequent incursions from the north occur when the beach may be strewn with *Spirula, Popita, Velella,* and other tropical and subtropical forms.

TABLE 10

PERCENTAGE OF DIATOMS OF DIFFERENT SPECIES FROM INSHORE WATERS NORTH ISLAND WEST COAST BEACHES DURING THE MONTHS OF MAXIMUM FLOWERING, 1939-44. CHAETOCEROS AS COLONIES, OTHERS AS CELLS

Beach	Period	Species								
		Chaetoceros armatus	*Asterionella japonica*	*Biddulphia*	*Thalassiothrix*	Coscinodiscinae	*Melosira*	*Rhizosolenia*	*Thalassiosira*	Others, Including Detritus
Ninety-mile	May-Sept.	72	23	—	3	—	—	1	—	1
North Kaipara	May-Sept.	89	10	1	—	—	—	—	—	—
Muriwai	May-Sept.	49	29	2	1	5	10	—	3	1
Wellington	Oct.-Dec.	26	60	1	4	1	—	—	—	8

VII. CONTROL OF TOHEROA STOCKS

The knowledge of fluctuating populations indicates that conservation measures will often fail. Some controls, however, have good prospects of increasing stocks and diminishing the serious effects of major changes caused by gales, mortalities, and migrations. If methods of improving the yield given below are followed production may be substantially increased.

From 1934 to 1946 the Wellington beaches were never exploited so thoroughly as the Ninety-mile, but one period occurred in 1940 when no toheroa were to be found on the Wellington beaches. However, the beds became restocked within 12 months when the migration off shore, which took place in 1939, was reversed. Had there been unrestricted digging it is probable that few toheroa would be found there today. There is no evidence yet of inshore and off-shore movement on the North Auckland beaches, where young toheroa less than 3 mm long are deposited on the beach and develop to maturity, often with only a slight change in position. Other broods may be added each year or the original stock may exist almost entirely as a single year-group; when it dies the beach again becomes barren.

In 1939 there was a small population of old stock on the southern part of the Ninety-mile beach, with young toheroa on the middle section. Conservation of the young stock may have aided the re-population of the Ninety-mile, but, through the removal of this brood, which had a potential life of 3-4 yr, the intensity of spawning was greatly reduced, and, in fact, no successful setting of spat has been recorded for 7 yr. The reduction of stocks on the south end was, however, the cause of the great resurgence of tuatua during 1940-45. They advanced about 5 miles northwards each year until at least 25 miles of beach were covered. Plate 5, Figure 2, shows how this beach was dug during the 1943 season, and, because of lack of suitable transport, opening operations were performed on the beach. The shells were left to wash over the toheroa beds. The movement of any hard material other than sand which the syphons can withstand is believed to have unfavourable effects on toheroa.

Although the beach was hard and with little seepage prior to the tuatua occupation, the tuatua beds produced the same type of features which characterize a dense toheroa bed, viz. several layers of shellfish, the upper one often projecting above the surface, and a wetness of the sand due to the slow loss of liquid produced by movement of the shells in breathing or digging in the sand.

The occasional disappearance of toheroa beds, which usually cannot definitely be traced to another part of the beach, occurs through changes in the beach; the permanent position of the stocks in the half-tide zone shows that as the beach changes so do the toheroa move. Moreover, although there is a slight movement north of some large toheroa, there is no evidence that beds move more than a few yards at a time, unless the beach becomes uninhabitable because of drifting sand or heavy seas. The manner in which toheroa form into dense beds suggests some form of attraction. The small immature size at which this may occur shows that initially the attraction is not for spawning; and the way in which whole beds of small toheroa move indicates a unity of purpose which is usually associated with creatures which move about actively. The movement of large toheroa at night favours a theory of migration at least partly under control of the animal. On the other hand the way in which shells become misshapen through overcrowding, and the reduction in growth rate in dense beds, suggest that migrations are made only when some peculiar condition of the beach occurs. Whether this is associated with wave action, hardness of the sand, or food supply is not known.

Congregation of toheroa into thickly populated areas naturally facilitates harvesting; the degree of dispersal varies for each beach. The Wellington beds consistently show the lowest population density over long sections, and 20 toheroa per sq. yd., which is about the average on this beach, may be near the minimum at which stocks can successfully reproduce. Where food is scarce, the sparsely populated beaches produce a better-conditioned shellfish than do heavily stocked beaches.

An examination of the numbers extracted in relation to the age composition of the stock gives some indication of the quantities which each beach may be expected to yield. The Wellington stock attains a maximum age of about 10 yr, which accords with an annual mortality in excess of 15 per cent. Weekly extractions in 1940, when there were good supplies, exceeded 10,000 for at least 20 weeks per year. At this period the total number over 3 in. was about 2,500,000, ranging from 2 to 10 yr old. The extractions of 200,000 per year approximate to the observed total annual mortality; for a period of abundance this is high but there is little evidence to show that it is too high.

On the North Kaipara beach in 1938, a year after the heavy mortality, the population was only slightly less than the optimum, although the size was small. Twenty miles of this beach, comprising the principal toheroa-bearing area, have produced about 400,000 toheroa or approximately 40,000 lb of meats annually, for many years (because of the increased activities of tourists the quantity canned declined in 1952-53 when 32,000 and 16,500 lb respectively were produced).

The reduction of stock which occurs on this beach, about 40 per cent. annually, indicates that some profitable use may at times be made of the dense beds of pipi toheroa, of which only three in 20 reach 4 yr of age (Rapson 1952). Transplanting those less than 1 in. long to other areas may be practicable. The great numbers of small shellfish which occur indicate that indiscriminate digging or disturbing of the spatting grounds may do much harm, as a bed 50 by 100 yd, with a density of 1000/sq. ft., contains nearly 3,000,000 toheroa.

The wastage which may occur through not utilizing stocks was seen under the conditions which existed at Muriwai in 1937, when beds were densely populated and were continuous on one section of beach, with relatively short intervals, for more than 5 miles. After the mortality in 1938 (which literally decimated the stocks) there were again good supplies in 1942, and, although there were practically no extractions for the best 25 miles of the beach, stocks were accumulated much more slowly after 1942. By 1945, however, conditions were comparable to 1937. There were no extremely long dense beds, but there were good stocks for nearly 25 miles compared with only 15 miles in 1937. The evidence from feeding indicates that the 1942 population was a reasonable maximum for Muriwai to carry, and a total population of three-quarters of that in 1937 is suggested as the optimum for the whole beach. An estimate of the productivity of this beach under such conditions is an annual yield of 600,000 toheroa from 20 miles of beach. In growing conditions as they existed in 1939-42 this number would produce approximately 30,000 lb of meats (based on 5 lb of meat per 100), a quantity considerably less than for the best 20 miles of the North Kaipara beach. Muriwai, however, might produce a much better type of stock if a regular digging programme were followed. The contour of the inshore bottom of the ocean is similar to that off the North Kaipara beach, so that a short-lived stock will always occur.

In Table 7 the productivity of the beaches, based on extractions from the North Kaipara beach, supply of food, and growth rate, is estimated at 150,000 lb of meats per annum. For completeness Ninety-mile is included using data obtained in 1939. It is expected that the tuatua will vanish from this beach and be replaced again by toheroa.

Tiller, Glude, and Stringer (1952) said that, although the total value of clam meat is small compared with production from other resources, the price per pound exceeds that of all other sea foods except lobsters. A substantial improvement in productivity of the toheroa beds might be achieved by the adoption of measures suggested below:

(1) The effect of dispersal north of eggs, larvae, and young stages will be minimized if the southern end of each productive area is kept well stocked by planting or other conservation measures. The most important positions in this respect are at the Waipapakauri Road on to the beach, and about 5 miles north of the Road on to the beach at Muriwai Rocks. The North Kaipara beach receives much natural protection at the south end, which is particularly inaccessible.

(2) It is desirable to leave large areas of the beach undisturbed, particularly at the southern end.

(3) Dense beds should be thinned to about 100 toheroa over $3\frac{1}{2}$ in. long per sq. yd., since growth rate will be increased where there is ample food, and where the latter is scarce a reduced toheroa population will be better sustained. Where beds contain mainly toheroa $1\frac{1}{2}$-3 in. long thinning is not considered necessary unless the density exceeds 400 per sq. yd. Transplanting would be most successful if specially designed trays were used.

(4) A 25 per cent. greater production may be achieved by canning toheroa only when in the best condition.

(5) In digging commercially or for thinning, strips about a yard wide should be dug with a similar area between them left untouched.

VIII. ACKNOWLEDGMENTS

The records of diatom occurrences are based on 10 representative samples kindly identified by Mr. P. S. Conger, of the Smithsonian Institution, United States National Museum. Mr. E. W. Meredith has given considerable data on toheroa occurrences, and assisted by collecting phytoplankton. Mr. E. R. Grimmet, of the New Zealand Department of Agriculture, expedited the analyses of water samples. Dr. Harold Thompson, Chief, Division of Fisheries, C.S.I.R.O., made available facilities for completing the work at Cronulla and has given valuable advice. The field work was carried out by the writer as Biologist to the New Zealand Government Marine Department, Wellington.

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EXPLANATION OF PLATES 1-5

PLATE 1

Fig. 1.—Toheroa marks left on a well-stocked beach. Holes left by both inhalent and exhalent syphons can be seen.

Fig. 2.—Marks made by large numbers of annelid worms which are sometimes mistaken for dense toheroa; the surface holes, however, are smaller, being only 1-2 mm diameter. Such areas are unsafe for motor vehicles.

PLATE 2

Fig. 1.—Toheroa shells left on Waiterere beach, Wellington, after the serious mortality; a few syphon holes of dead toheroa may be seen also; Jan. 1938.

Fig. 2.—Toheroa, Muriwai beach, unable to cover themselves completely. Incipient mortality recorded on three beaches, November 1938.

PLATE 3

Fig. 1.—A "lethargic" toheroa unable to dig into the sand. Note the limp inhalent and completely relaxed exhalent syphon.

Fig. 2.—Deposit of tuatua shells 4 ft thick, Mangonui Bluff, Ninety-mile beach, 1939. The shells are not tightly packed on the exposed face and cannot be distinguished from recently dead shells from the beach, size ranges from 1½ to 2½ in.

PLATE 4

Fig. 1.—Method of survey showing relatively narrow toheroa zone on a wide beach. Hukatere, Ninety-mile beach, 1939.

Fig. 2.—Layer of phytoplankton left as the tide recedes. In places it is over an inch thick. Note the toheroa bed, left foreground, and seepage water from sand cliffs, left background (cf. Plate 5, Fig. 1).

PLATE 5

Fig. 1.—Phytoplankton becoming concentrated on the beach by the incoming tide from surface scum; often there is much more in the water than floating on the surface.

Fig. 2.—Method of harvesting toheroa, Ninety-mile beach. Digging started at several places on the seaward side of the bed.

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FEEDING AND CONTROL OF TOHEROA

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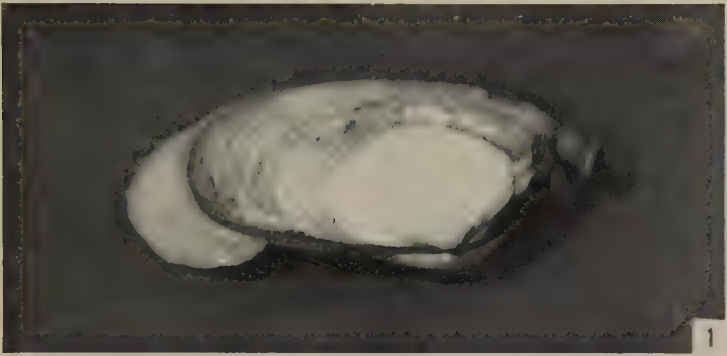

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FEEDING AND CONTROL OF TOHEROA

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FEEDING AND CONTROL OF TOHEROA

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SOME USES OF PROBABILITY PAPER IN THE ANALYSIS OF SIZE FREQUENCY DISTRIBUTIONS

By R. M. Cassie*

(*Manuscript received March* 12, 1954)

Summary

Methods are described by which the component groups may be extracted from polymodal size frequency samples by the use of probability graph paper. Four examples are given illustrating: the solution of a distribution with more than two modes and with only one exposed flank; the coordination of fish age determinations by the two methods, length frequency analysis and scale reading; a bivariate sample where the two means coincide though the standard deviations are different; a method of correcting for truncation.

I. Introduction

A method by which probability paper may be used in solving bimodal or polymodal frequency distributions has been described by Harding (1949). More recently this technique has been extended (Cassie 1950) in a manner which eliminates much of the trial and error necessary in the original method when more than two normal distributions are involved. Once the points of inflexion have been picked, the process becomes a purely mechanical one which can often be passed to the laboratory technician for completion. Some further useful applications have since come to light, and in describing them, since the 1950 paper is not readily available, the method will be briefly recapitulated. The process is reminiscent of that described by Buchanan-Wollaston and Hodgson (1929), in that each normal curve is fitted (either graphically or arithmetically) by means of its exposed flank, i.e. the part which does not overlap with its neighbour. Once the first curve has been so eliminated, the flank of the next becomes exposed and the process may be repeated. The arithmetic method involves the fitting of a series of parabolas to the logarithms of the frequencies. However, it is often difficult to determine which points in any one component are free of contamination by its neighbours. The use of probability paper gives a linear transformation (equivalent to the probit, commonly used in biological essay) which allows the overlapping flanks to be more readily detected, thereby giving a wider range of points which may be used in curve-fitting.

It should be noted that raw data only are employed in all the following examples. It is not legitimate to smooth since the parameters so obtained will be biased and tests of significance become invalid. As a rule, however, the points automatically assume a regular appearance when plotted in this manner even when the corresponding frequency polygon has a pronounced

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* Fisheries Research Laboratory, Marine Department, Wellington, N.Z.

"saw-tooth" form. Occasionally, where the loss of too much information will not result, it may be found convenient to group in larger class intervals, though this is seldom necessary.

II. Example 1

Figure 1 shows the cumulative percentage distribution of length of a catch of 256 snapper (*Chrysophrys auratus* Forster) taken by a trawl with a mesh of about 1½ in.* The points (circles) form three distinct points of inflexion at 10, 66, and 91 per cent., and a fourth, less plain, at 98.6 per cent. The first or "0" (strictly speaking 0+) year-class is extracted as explained by Harding (1949), by multiplying the original percentages up to the point of inflexion by 100/10.

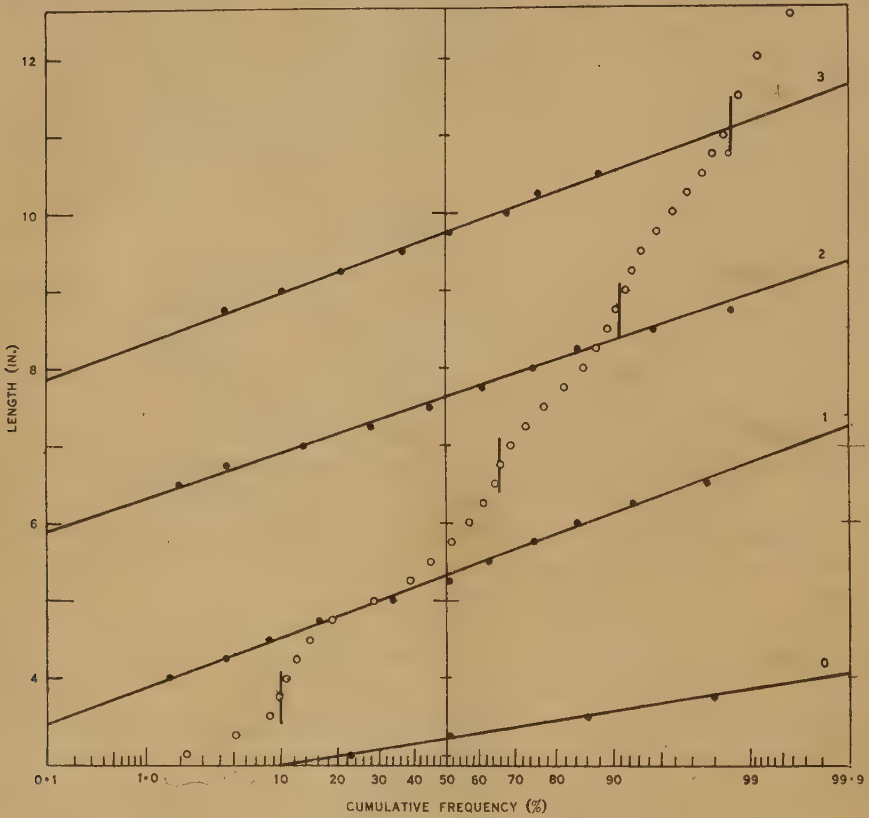

Fig. 1.—Cumulative percentage length distribution of 256 snapper.

Thus for the first point 2.3 per cent. × 100/10 = 23.0 per cent. A straight line can be readily fitted to the new points (dots). As there is little or no overlap between the "0" and "1" year-classes, the next portion of the curve can be fitted in a similar manner, except that 10 must be subtracted both from the original percentage and from the numerator of the multiplying term:

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* The original data have been slightly modified to simplify explanation, though the conclusions and test of significance are unaffected.

e.g. for the first point beyond the inflexion,

$$(10.9 - 10.0) \times 100/(66 - 10) = 1.6 \text{ per cent.}$$

In this case the last of the new points lies somewhat to the right of the fitted line. This is due to overlap with the "2" year-class and is a normal occurrence. The greater the degree of overlap, the greater the number of such points. This implies, firstly that the fitting of the "2" group may be commenced below the point of inflexion, and secondly that a correction must be made to the first few points. Taking the point at 64.8 per cent. just below the inflexion, the percentage at the same level on the "1" curve is 97.0 per cent. The percentage of the total represented by the "1" component will then be

$$97(66 - 10)/100 = 54.3 \text{ per cent.}$$

Add to this the 10 per cent. represented by the "0" year-class

$$54.3 + 10.0 = 64.3 \text{ per cent.}$$

The first new point on the "2" curve will then be

$$(64.8 - 64.3)100/(91 - 66) = 2.0 \text{ per cent.}$$

This process continues until at the third point above the inflexion the percentage on the "1" curve is 99.9, or nearly 100, and the correction

TABLE 1

Year-class	m	s*	Percentage of Total	n
0	3.22	0.27	10	25.6
1	5.33	0.62	56	143.4
2	7.62	0.56	25	64.0
3	9.74	0.60	7.6	19.4
4+	—	—	1.4	3.6
			100.0	256.0

where m = mean length (in.),
s = standard deviation (in.)*,
n = number in year-class.

$\chi^2 = 10.3$
$P = 0.5$
d.f. = 12

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* The standard deviation may be determined by measuring the difference between the mean and the 15.87 or 84.13 per cent. level on the graph curve. Since this level is not normally shown on the paper, some may find it easier and more accurate to measure to the 99.99 per cent. level at the edge of the paper and divide by 3.72: e.g. for year-class 1:

50%	5.33
99.99%	7.63

$$2.30/3.72 = 0.62.$$

need no longer be applied. The new point will then be

$$(73.4 - 66.0) \times 100/(91 - 66) = 28.6 \text{ per cent.}$$

Fitting the "3" group proceeds in exactly the same manner, while above the last point of inflexion there are only three points, representing the same number of fish, so that the analysis is terminated at 98.6 per cent.* The results of the analysis are shown in Table 1.

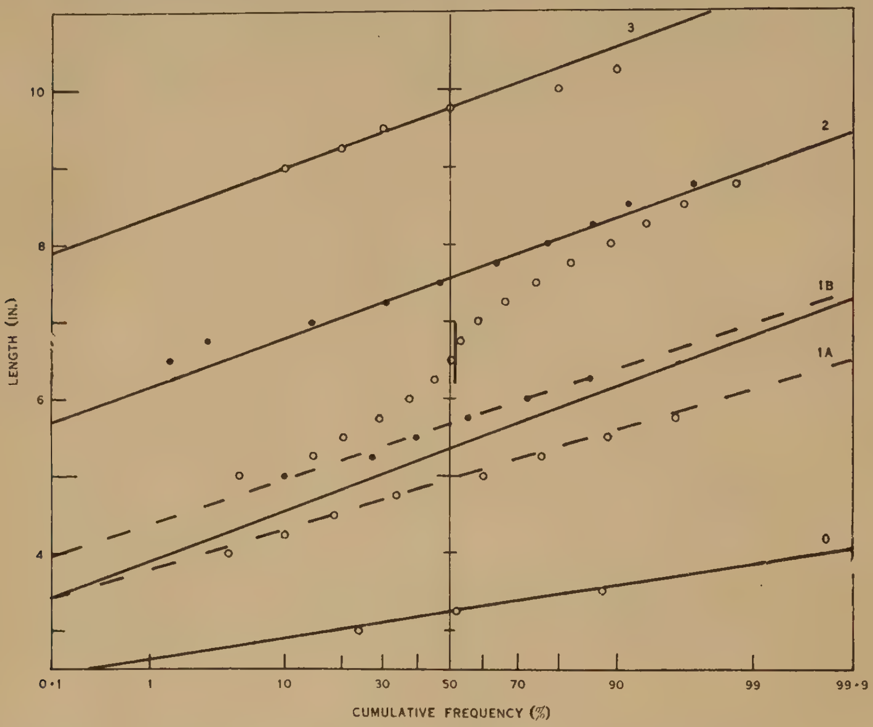

Fig. 2.—Scale reading data plotted against linear curves from Figure 1.

The standard deviations of the three older year-classes are almost identical, but that of the "0" class is much smaller. This is due to truncation at the lower end of the distribution since the mesh of the trawl was not fine enough to capture the smaller fish. It will be shown below (example 4) that a correction may sometimes be made for truncation. However, the sorting action of a trawl is often such that a large piece may be removed from a size distribution without apparently affecting its normality. The true mean of the "0" class is almost certainly lower and the standard deviation higher than this sample would suggest.

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* Note that if these three points had been omitted or added to, the analysis would have produced the same results, though the percentages represented by the original points would have been different. This fact may often be used to simplify the mechanical calculations. If the total number, N, of the sample is nearly 100 (or can be made nearly 100 if divided by a simple factor) the cumulative frequencies may be plotted without conversion to percentages: nine, e.g., if $N = 309$, divide by 3 (provided the largest fish are not required in the analysis).

Classes "1" and "2" both have slight inflexions near the centre, suggesting that they might possibly be bimodal, though there is not sufficient evidence to warrant adding further complexity to the solution by subdividing them.

III. EXAMPLE 2

In collecting the sample described in the first example, scales were taken from each fish as it was measured. The results of scale reading are shown in Table 2.

TABLE 2

RESULTS OF SCALE READING

	m	s	n
0	3.22	0.25	25
1	4.91	0.49	71
2	6.58	1.11	138
3	9.68	0.46	10

The estimates for classes "0" and "3" do not differ significantly from the length frequency determination. The smaller value of n for the latter is due to the fact that some scales were not readable. On the other hand, quite different estimates are obtained for classes "1" and "2". In Figure 2, the scale reading data (circles) are plotted against the linear curves from Figure 1. The "1" class, though displaced, is still unimodal (broken line, 1A) but the "2" class has a pronounced point of inflexion at 52 per cent. The points of the two components are shown as dots, the upper one fitting very closely the "2" curve from Figure 1 while the lower one (broken line 1B) falls a little above the "1" line. The group originally classed as "1" has now resolved itself into the components shown in Table 3.

TABLE 3

	m	s	n
1A	4.91	0.49	71
1B	5.64	0.55	72

Pooling these figures gives $m = 5.27$, and $n = 143$, both of which are virtually identical with the values for the original "1" group.

The information derived from examples 1 and 2 allows a choice of two explanations regarding the age composition of the catch. Either half the scales classed as "2" in Table 2 have one false ring and the fish they represent are actually a year younger; or the age-class "2" is bimodal owing to a second late spawning 2 yr ago, or to a second snapper population with a lower growth rate. The analysis shown here does not, of course, offer any solution to this question, though other information of a similar type suggests strongly that the first alternative is the correct one, and the two lines 1*A* and 1*B* have been labelled accordingly.

IV. EXAMPLE 3

It sometimes happens that two normally distributed populations are mixed, both with the same (or almost the same) mean, but with different standard deviations. Such a case is shown in Figure 3, the length frequency of 63 snapper meshed in the cod-end of a trawl. The reversed S-shape of the curve indicates positive kurtosis*, which is typical of this type of distribution. The two component populations in this example are probably due to the two different ways in which a fish can become meshed. Firstly there are those which are caught by the twine passing behind the posterior edges of the gill covers. These fish are held very tightly indeed and have virtually no chance of escape, though on the other hand only a very limited range of sizes is susceptible to capture in this way. Secondly there are those caught either by the head or body. A much wider size range may be taken thus but, since the holding point is less secure, many escape again. In this case there is probably little

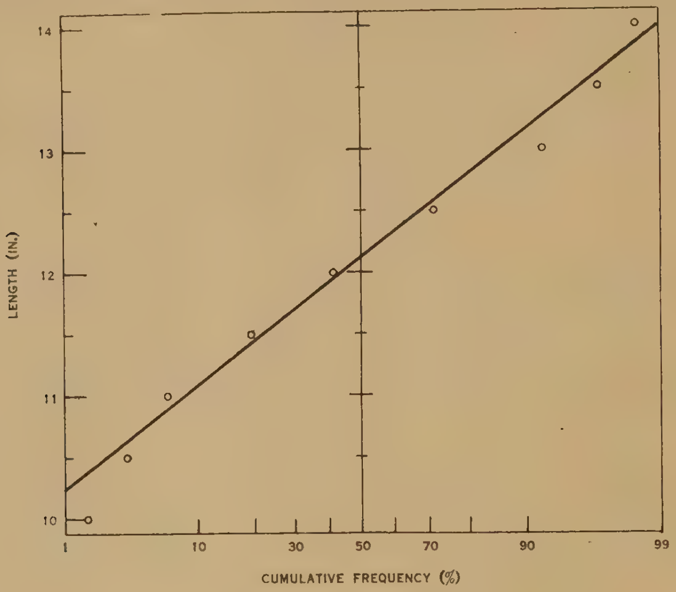

Fig. 3.—Length frequency of 63 snapper in trawl cod-end.

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* The four different deviations from normality may be identified as follows in the probability curve:

Positive skew: slope increases from left to right; negative skew: slope decreases from left to right; positive kurtosis: curve a reversed S-shape; negative kurtosis: curve S-shaped.

to be gained by separating the two components, although this might be done if necessary by a process of trial and error. However, if a number of such distributions were to be compared, say the catches of different gill-nets, the interpretation of results might be greatly facilitated by the knowledge that two populations (in the statistical sense) are present, and may vary independently of each other under different circumstances.

V. EXAMPLE 4

A further source of obscured normality occurs when the sample has been truncated at one or both ends. Figure 4 shows the distribution of shell length of a sample of 64 toheroa (*Amphidesma ventricosum* Gray) taken from a beach at the age of a few months. It was known that the collector was searching particularly for small specimens and in doing so was likely to neglect those at the upper end of the size range. At the same time the very smallest shells, being less than $\frac{1}{4}$ in. long, were somewhat difficult to find, so that it was suspected that the distribution might be truncated at both ends. It was also known that the parent stock frequently has more than one burst of spawning during the summer months, and that there might be a polymodal age-class. The distribution (circles) has a point of inflexion at about 52 per cent. Separating into components gives two sets of points (circles with dots), both of which are

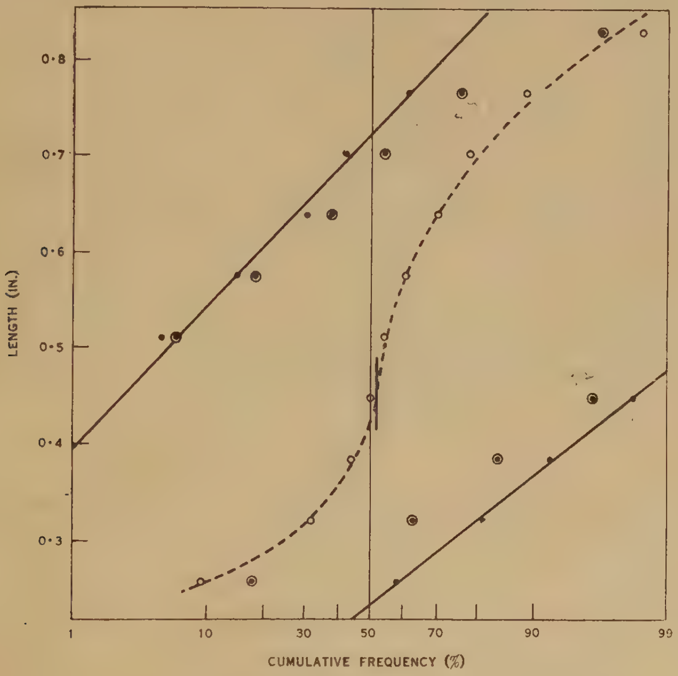

Fig. 4.—Shell length distribution of 64 toheroa.

skewed, the lower positively, the upper negatively, by truncation. A correction may be made by applying point by point the equation

$$P' = p + p'' - pp''/100,$$

where P' = corrected percentage (cumulative from truncated end),
p = uncorrected percentage (cumulative from truncated end), and
p'' = percentage of group lost by truncation.

In Figure 4 truncation is approximately 50 per cent. for the lower curve, and 20 per cent. for the upper.* Straight lines can now be fitted by eye to the corrected points (dots), giving the results shown in Table 4. The resultant curve, drawn in Figure 4 as a broken line, fits the original data very well.

TABLE 4

	m	s	n	%	n'	%′
Second spawning	0.23	0.11	31	48	39	37
First spawning	0.72	0.14	33	52	66	63

$\chi^2 = 1.45,\ P = 0.5,\ d.f. = 2$

where n' = estimated value of n if sample were not truncated
%′ = estimated value of % if sample were not truncated.

The usual tests of significance of differences between means or standard deviations may be applied if necessary when these differences are small. Goodness of fit for the whole sample may be tested by constructing an expected frequency distribution, using the estimated parameters in conjunction with a table of the ordinates of the normal distribution (e.g. Fisher and Yates 1953) and computing χ^2 in the normal manner. As three degrees of freedom are lost for each new component

TABLE 5
EXAMPLE 1

Length (in.)	Frequency	Length (in.)	Frequency	Length (in.)	Frequency	Length (in.)	Frequency
$2\frac{7}{8}$	6	$5\frac{3}{8}$	17	$7\frac{7}{8}$	9	$10\frac{3}{8}$	2
$3\frac{1}{8}$	7	$5\frac{5}{8}$	17	$8\frac{1}{8}$	6	$10\frac{5}{8}$	1
$3\frac{3}{8}$	9	$5\frac{7}{8}$	14	$8\frac{3}{8}$	4	$10\frac{7}{8}$	1
$3\frac{5}{8}$	3	$6\frac{1}{8}$	11	$8\frac{5}{8}$	3	$11\frac{1}{8}$	—
$3\frac{7}{8}$	3	$6\frac{3}{8}$	8	$8\frac{7}{8}$	3	$11\frac{3}{8}$	1
$4\frac{1}{8}$	4	$6\frac{5}{8}$	4	$9\frac{1}{8}$	2	$11\frac{5}{8}$	—
$4\frac{3}{8}$	6	$6\frac{7}{8}$	7	$9\frac{3}{8}$	2	$11\frac{7}{8}$	1
$4\frac{5}{8}$	11	$7\frac{1}{8}$	11	$9\frac{5}{8}$	4	$12\frac{1}{8}$	—
$4\frac{7}{8}$	26	$7\frac{3}{8}$	11	$9\frac{7}{8}$	3	$12\frac{3}{8}$	1
$5\frac{1}{8}$	24	$7\frac{5}{8}$	11	$10\frac{1}{8}$	2	$12\frac{5}{8}$	1
						n	256

---

* The degree of truncation can usually be judged fairly readily after some experience, although sometimes several trials must be made to obtain the best value.

extracted from the population, it will be obvious that the simplest possible solution will be the most likely to give a good fit. Such tests may often be dispensed with by the biologist once he is sufficiently familiar with the technique to judge from experience when significant deviations are likely to be present. He may also have other information derived from previous data which will assist in making this decision.

TABLE 6

EXAMPLE 2

Length (in.)	0	1	2	3	Length (in.)	0	1	2	3
2⅞	6				7⅞			9	
3⅛	7				8⅛			6	
3⅜	9				8⅜			4	
3⅝	3				8⅝			3	
3⅞		3			8⅞			2	1
4⅛		4			9⅛				1
4⅜		6			9⅜				1
4⅝		11			9⅝				2
4⅞		19	7		9⅞				3
5⅛		11	13		10⅛				1
5⅜		9	8		10⅜				1
5⅝		5	12		10⅝				
5⅞		2	12		10⅞				
6⅛		1	10		11⅛				
6⅜			8		11⅜				
6⅝			4		11⅝				
6⅞			7		11⅞				
7⅛			11		12⅛				
7⅜			11		12⅜				
7⅝			11		12⅝				
					n	25	71	138	10

Being graphical, the method does not give the best possible solution but in those cases where it is most useful the errors are usually small compared with the standard errors of the sample parameters. If greater precision were required, the probability paper solution might be used as a first approximation in an iterative solution by an arithmetical method. Most biologists will not find such a refinement necessary, and indeed Pearson (1894) and others since have found the arithmetical dissection of even the simplest multivariate distributions a prodigious task, scarcely likely to be undertaken by any but the professional mathematician.

It does not, of course, follow that every continuously variable biological population can be described in terms of the normal distribution. Any such solution is only of value when some physical significance can be ascribed to the components (e.g. different age-groups or sexes).

Nevertheless, the simple and rapid precaution of plotting on probability paper sometimes reveals unsuspected features in even the most apparently simple distributions. For those who may wish to verify the solutions given in the examples the relevant data are given in Tables 5-8.

TABLE 7
EXAMPLE 3

Length (in.)	Frequency
9¾	1
10¼	1
10¾	2
11¼	8
11¾	14
12¼	19
12¾	13
13¼	3
13¾	1
14¼	—
14¾	1
n	63

TABLE 8
EXAMPLE 4

X	Frequency
3	6
4	15
5	7
6	4
7	3
8	4
9	6
10	5
11	7
12	6
13	1
n	64

Length = (X + 0.5)/0.064 in.

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